

I. *On the Evolution of the Vertebral Column of Amphibia and Amniota.*

By HANS GADOW, M.A., Ph.D., F.R.S.

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INTRODUCTION.

THIS paper, with that by Miss ABBOTT and myself ('Phil. Trans.', B, 1895), forms a rounded-off investigation of the evolution of the vertebral column. I have to thank Miss ABBOTT for the preparation of sections and for hundreds of preliminary consecutive drawings of *Salamandra maculosa*, *Triton critatus*, and of *Hyla septentrionalis*.

Mr. H. H. BRINDLEY most generously placed at my disposal an enormous number of sections through the tails of embryos and adults of *Hoplodactylus pacificus*, *Platydactylus gleadovi*, and of *Lacerta vivipara*, which he had already prepared for some other occasion.

Fossil specimens of unknown composition can be satisfactorily studied only by autopsy; photographic reproductions are mostly useless for detail; if the specimens are drawn by hand, the mental bias comes in, and it is difficult to say whether that of the artist or that of the author is the stronger. However, FRITSCH's volumes deserve the highest praise; his method gives admirable results, namely, the method of electrotyping the minute originals and then to enlarge the photographs which have been taken from the casts.

I have seen and handled all I possibly could of fossil Amphibia and Reptilia, chiefly through the courtesy of Mr. ANDREWS and his chief, of the Geological Department of the Natural History Museum.

Professor K. v. ZITTEL had the kindness to lend me the original specimens of *Archegosaurus*, described by v. MEYER. Professor A. GAUDRY, in reply to some questions, wrote me a letter which was nothing less than an explanatory discourse.

In the course of this research it became more necessary than ever to learn the range or amplitude of the modifications of the various elements which enter into the composition of vertebræ. The extreme variations are not necessarily the exceptions, more or less abnormal, and therefore to be passed over in silence. On the contrary, this procedure in the gathering of facts, often revealed as truly normal and important what had hitherto been considered as insignificant detail. This applies, in the selection as types, to the individual specimens, and still more forcibly to the larger groups, as e.g., families from and for which we select the representatives.

The frog is the most glaring example. It possesses scarcely anything typical, which is also applicable to any other group of vertebrata.

I have abstained as much as possible from discussing and arguing out some of the many contentious questions at issue in this paper, but I have tried to show how certain errors have arisen.

For the rest, for the correctness of the views taken in this essay, the facts themselves must speak. The literature is so bulky and scattered, and the material required is so vast and by no means always at hand, that it seemed advisable to give a great number of illustrations. These are mostly drawings in outline and slightly diagrammatic, but they are correct and are taken from actual specimens.

URODELA. (Figs. 1-14.)

Transverse sections through the vertebral column of metamorphosing larvæ show the following structures.

The bulk of the *chorda* is composed of large cells which form a wide vacuolated meshwork with marginal nuclei, and a considerable amount of cell-protoplasm. Near the outer rim of the *chorda* lies the usual layer of smaller cortical cells; this *chordal epithelium* persists longest, even throughout life, in the Perennibranchiata, but, in the

Salamandridæ, it becomes indistinct during the metamorphosis, being then, by loss of the cell protoplasm, reduced to a thin epithelium with small nuclei interspersed.

The *chordal sheath*, a cuticular product of the chorda itself, consists of a distinct *Elastica interna*, of either homogeneous or slightly conventional lamellar aspect, and the *Elastica externa*. The latter is thickest in the Perennibranchiata. It appears, when shrinkage of the *E. interna* has taken place, as an undulating line. The whole sheath, although conspicuous, is decidedly weak, reminding us of that of osseous Ganoids, in opposition to Dipnoi, cartilaginous Ganoids, and Elasmobranchs. The thickness of the sheath is by far greater in the intervertebral than in the vertebral or intravertebral region, owing to the reduction of the *Elastica interna*. The *E. externa* is always present, although, at best, only an extremely thin membrane of strong refracting power, it is sometimes not easily seen, especially in the intravertebral region, when it is the only structure which separates the chordal epithelium from direct contact with the cartilaginous and ordinary connective tissue of the skeletogenous layer.

The *skeletogenous layer* produces and contains the cartilage; whatever of this whole layer remains membranous, or is transformed into ordinary fibrous connective tissue may, for brevity's sake, be spoken of as the *Membrana reuniens*. Outer and inner portion of the skeletogenous layer are terms which are less advisable, because the "inner portion" is liable to be confounded with the pervaded chorda-centra forming chordal sheath of Dipnoi and Elasmobranchs; *c.f.* 'Phil. Trans.,' B, 1895, p. 177, and fig. 28, p. 176.

It is clear that the "membrana reuniens" comprises eventually the perichondrium, and is externally continuous with the intermuscular septa.

In transverse and in longitudinal sections the cartilage of the neural arches can be seen to be completely surrounded by, or enclosed as in a bag, by the same membrana reuniens which covers the intervertebral cartilage; but there is this slight difference, that the outer peripheral surface of the intervertebral cartilage is covered by a thick layer of connective tissue, while, on the inner median surface the enclosing *outer* lamella of the membrana reuniens is reduced to the perichondrium only. Again, the membrana reuniens on the outside of the neural arches appears less conspicuous than it does upon the intervertebral cartilage, while, below the bases of the arches, the respective *inner* lamella of the membrana reuniens is thicker than the inner lamella enclosing the intervertebral cartilage. In other words, the inner lamella of the membrana reuniens, which intervenes between the cartilage and the *Elastica externa*, is much more conspicuous in region of the cartilage of the neural arches than of the intervertebral cartilage. Hence, it comes to pass, that these two cartilages seem to lie in different levels, and this mistaken feature seems to have caused the various natural, but futile attempts of homologizing the intervertebral ring of cartilage in the Amphibia with the ring of cartilage which produces the vertebral centra of the Dipnoi and Elasmobranchs.

GEGENBAUR, who in 1862 had discussed this view as imaginable, properly abandoned it in 1867 (Lepidosteus paper) and insisted upon the same origin of the intervertebral cartilage with that of the arches. It should be remembered that the origin of the chorda-centrous cartilage was discovered twenty years later, namely, by LVOFF, shortly after to be appreciated and further expounded by ZYKOFF, KLAATSCH, and in the conjoint paper by Miss ABBOTT and myself.

Lastly, portions of the membrana reuniens seem to have been mistaken for the Elastica externa. For instance, by HASSE (Lit. No. 57), on Plate 2, fig. 10, the layer named *c.sc.*; in fig. 13 this layer is represented with a thickness which the true Elastica externa never attains, namely, an elastic membrane whose chief function seems to be the nutrition of the chorda by osmosis. Again, on Plate 3, in figs. 19 and 20, which show the differences between inter- and intravertebral sections very well indeed, the thick black zone, named *c.sc.*, is not the E. externa, but the dense inner stratum of the M. reuniens, which is surrounded externally by tissue already calcifying. Lastly, in fig. 21, the true E. externa is represented, but not named.

It is obvious that, owing to removal of the E. externa, which is the very landmark between the chorda with its derivatives, and the skeletogenous layer, the synonymy has become somewhat complicated and perplexing;* moreover, it is now clear that HASSE quite consistently treats the intervertebral cartilaginous ring as an intercuticular structure, and, consequently, as homologous with the centra of Elasmoderms.

Here may follow a few measurements of the thickness of various layers, in the 3 centims. larva of *Salamandra maculosa*, just metamorphosing.

Chordal sheath, trunk. Intervertebral region, 0·022 millim. Intravertebral region; too fine to be measured, less than 0·001 millim.

"	"	tail.	"	"	0·012	"		
Whole skeletogenous layer, trunk. Intervertebral region, 0·025 millim.								
"	"	"	tail.	"	"	0·056	"	of which the cartilaginous zone measures 0·046 millim.
"	"	"	trunk.	Intravertebral	"	0·005	"	

* *Synonyms* concerning Amphibia.

Chordal epithelium, Chorda-epithel. Most authors since GEGENBAUR.

Chordal sheath inclusive of E. interna and E. externa = Cuticula chordæ, FIELD.

Elastica interna = Cuticula chordæ s. Elastica interna, HASSE, FIELD.

= Faserige Chordascheide, LVOFF.

= Innere Scheide, GOETTE.

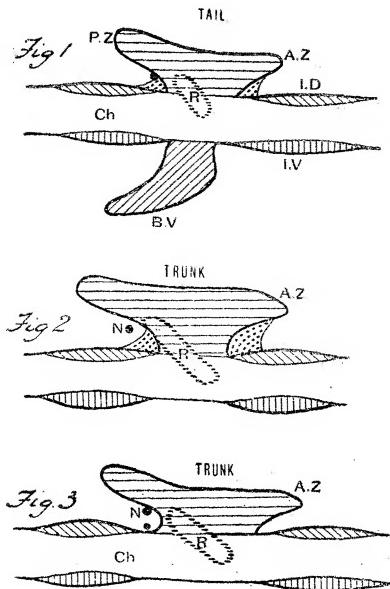
Elastica externa = E. ext., GEGENBAUR, LVOFF; also HASSE in earliest larvæ of *Triton*. Cuticula chordæ, FIELD.

Skeletogenous layer = Bindegewebige Scheide der chorda.

Membrana reuniens, i.e., outer non-cartilaginous portion of the skeletogenous layer = Cuticula skeleti s. Elastica externa, HASSE; Cuticula skeleti, FIELD.

Inner, cartilaginous portion of the skeletogenous layer = Intercuticulaere Scheide des skeletogenen Gewebes, HASSE.

The following is a general description of the development of the axial skeleton of *Triton* and *Salamandra*. It is easiest to begin with the tail, as the least modified part.



Figs. 1 and 2. Diagrammatic reconstruction of the tail- and trunk-vertebræ of a half-grown larva of *Triton cristatus*.

Fig. 3. Trunk-vertebra of a 5 centims. larva of *Salamandra maculosa*.

A.Z., P.Z. = anterior and posterior zygapophyses.

I.D., I.V. = interdorsalia and interventralia.

The extent of the attachment of the ribs is dotted in.

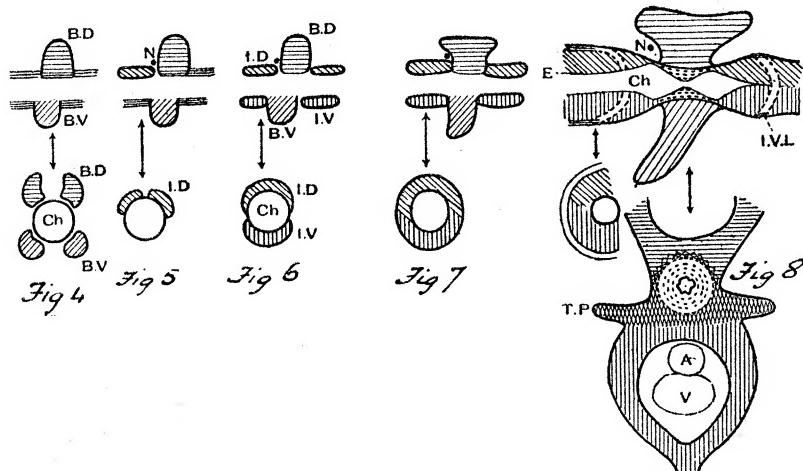
N. = position of the origin of the spinal nerve.

R. = Ribs, with the extent of their attachment dotted in.

At first the skeletogenous layer appears in the shape of a membrana reuniens, and is composed of indifferent, white connective tissue. Cartilage is rather tardy in making its appearance; there is, for instance, none in many larvae of 2·5 centims. in *Triton cristatus*. Then (fig. 4) it develops itself in the shape of dorsal and ventral arcualia; the latter lie, as a rule, in a level slightly more caudal than the dorsalia. The ventralia, basiventrals, ultimately meet and fuse with each other below the caudal vessels; somewhat later the basidorsalia, or neural arches, unite above the spinal cord. None of these cartilaginous basalia rest directly upon the Elastica externa, and their basal ends do not grow towards each other around the sides of the chorda, nor do they meet with their fellows above and below the chorda; they remain separate.

Next appears cartilage in the spaces between two successive arches, likewise in the skeletogenous layer, but in the immediate neighbourhood of the Elastica externa (fig. 5). This intervertebral cartilage shows itself first on the dorsal side, and close behind the dorsal arches; a little later (fig. 6) the interventral cartilage is developed, and, as it seems, in front of the basiventrals. These dorsal and ventral interbasalia rapidly meet and fuse into an intervertebral ring, which is thickest dorsally and ventrally, thinnest laterally. The formation of the intervertebral ring is accomplished rapidly; its constituent elements are not sharply marked, and they hurry through the following stages, indications of which appear now and then a little more clearly in long series of sections. First, the right and left interdorsals meet above the chorda and form a dorsal semi-ring; the interventrals produce a ventral semi-

ring. One dorsal and one ventral semi-ring meet and fuse into one complete ring, but, owing to the mode of appearance and the position of the semi-rings, it follows that the ventral semi-ring 10 fuses with the dorsal semi-ring 9, &c. Consequently, the intervertebral rings are bi-metameric, practically neutral zones.



Figs. 4 to 8. Diagrammatic representations of five stages of the development of caudal vertebrae of Urodela.

The upper series represents the vertebrae in vertical longitudinal sections, as seen from the right side; the lower series refers to transverse sections, the levels of the sections being indicated by the arrows.

Cartilaginous parts are indicated by ruled lines; calcified connective tissue in fig. 8, lower diagram, is cross-shaded; the thick black contours of fig. 8 indicate the outer bony mantle. The intravertebral cartilage in fig. 8 is indicated by the dotted area.

At the same time, the skeletogenous layer, so far as it intervenes between the Elastica externa and the dorsal and ventral arches, becomes calcified, and this process of calcification spreads rapidly through the rest of the skeletogenous layer wherever this is not cartilaginous. Thus it comes to pass that, firstly, the dorsal and ventral arches are firmly connected with each other by calcified tissue (fig. 8); secondly, that the intervertebral ring is surrounded by a continuation of the calcifying lamellæ of the skeletogenous layer. The intervertebral rings grow in thickness, naturally more so where they are not yet overlaid by the calcifying lamella, so that ultimately the cartilage assumes its greatest thickness in the region of the future intervertebral joints. Here the process of calcification stops for obvious reasons.

The calcification, proceeding from the middle of the vertebrae, and investing the intervertebral cartilage by its head- and tailward extension, produces two hollow cones, which meet point to point in the middle of the vertebra (*i.e.*, in the transverse level of the arches), while their bases coincide with the middle of the intervertebral cartilage (level of the future joint). When, lastly, the cartilaginous arches themselves are ossified, macerated vertebrae look strikingly like the biconcave vertebrae of many Teleostean fishes.

The invertebral ring of actively growing cartilage hinders the chorda in its further growth, reducing it to a thread (occasionally called funiculus chordæ), or even destroying it completely.

In many Urodela, especially in the Perennibranchiata, the whole intervertebral cartilage acts as the joint, being, in fact, a flexible mass intercalated between the bases of the hollow calcified cones of the successive vertebræ. However imperfect this joint may be, it does fulfil the requirements of these long-bodied and long-tailed aquatic Urodela.

Even in the more terrestrial Urodeles the formation of the intervertebral joint does not always lead to a complete severance of the cartilage, but, as GEGENBAUR has already fully described, only a differentiation of its cells takes place, while the inter-cellular substance remains continuous. Nevertheless, the cup of these potentially opisthocœlous vertebræ does calcify.

The formation of the joint cuts the whole cartilaginous ring, or septum, when the chorda has been destroyed, into two unequal portions. In the case of opisthocœlous joints the knob belongs, of course, to the anterior end of the vertebræ, and receives the larger share of the cartilage (see fig. 13, on p. 10).

Considering (1) that these joints are formed very late, after the ring has been completed, (2) that they often remain imperfect, and lastly, that the cups and balls lie in the axial centre of the column, it is impossible to say what share the original inter-dorsal and interventral elements take in the cups and balls respectively.

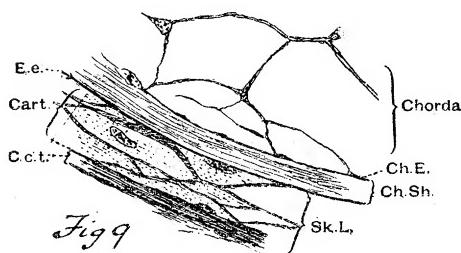
To judge from the general resemblance of these features with those of the larvæ of *Lepidosteus*, which is likewise opisthocœlous (see 'Phil. Trans.', B, 1895, p. 209, fig. 7), we might assume a similar arrangement; but in *Lepidosteus* the spinal nerves issue between two vertebræ, in level of the middle of the joint. In the Urodela the nerves arise and issue immediately behind the neural arches and in front of the intervertebral cartilage, i.e., intravertebrally in the finished vertebral column, agreeing in this most important respect with *Amia* ('Phil. Trans.', B, 1895, p. 207). It follows that the urodelous joints cannot be derived from those of osseous Ganoids; they are only analogous with them. Dipnoi and cartilaginous Ganoids are still acentrous, Elasmobranchs are chorda-centrous creatures. Consequently the joints of the Urodela are a new feature, acquired by these Amphibia themselves, not inherited from pre-amphibian, nor even from semi-amphibian ancestors.

The *vertebræ of the trunk* (figs. 2 and 3, see p. 5, and figs. 9–12) differ from those of the tail chiefly by the gradual suppression of the basiventral cartilage. As GOEPPERT has discovered this important fact, published in a preliminary paper in the last number of the 'Morphol. Jahrbuch' (Lit. No. 53), I refer to his results in a separate footnote.* I have been able fully to confirm his researches in *Salamandra*

* GOEPPERT has shown, that in the new-born larva of *Salamandra maculosa*, basal arcualia of hyaline cartilage occur in most vertebræ of the trunk. In most vertebræ these arcualia exist asymmetrically, either on the right or on the left side of the aorta; occasionally, however, they occur in pairs; they

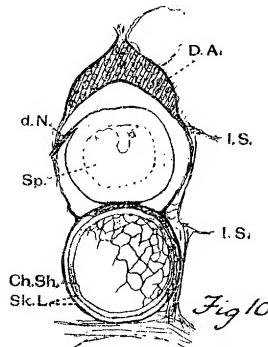
maculosa, and have only to add that the same gradual suppression can be shown by comparison of the macerated skeletons of many adult specimens of the *Axolotl*, *Menobranchus*, *Cryptobranchus*, *Salamandra*, and *Triton*.

Calcification, and later on ossification, appears in the intravertebral region of the skeletogenous layer surrounding the chorda, and passes continuously into the bases of the dorsal arches, the cartilage of which does not rest directly upon the *Elastica externa*. Thus is formed an intravertebral bony ring.



Portion of a transverse section through the intervertebral region of a larva of *Salamandra*. Strongly magnified.

- C.c.t.* = Calcifying connective tissue.
Ch.E. = Chordal epithelium.
Ch.Sh. = Chordal sheath.
E.e. = Elastica externa.



Transverse section through the trunk of a larva of *Salamandra*, in level of the origin of the dorsal root (*d.N.*) of a spinal nerve.

- Ch.Sh.* = Chordal sheath.
Sk.L. = Skeletogenous layer.
I.S. = Intermuscular septal tissue.

Owing to the smallness or absence of the basiventral cartilage, the capitular portion of the ribs (which, as in fishes, are the distal differentiated-off portions of the laterally-extending basiventral cartilages) is much reduced. The ribs appear therefore occasionally at some distance from the chorda, but they develop a tubercular knob, which meets a corresponding oblique cartilaginous outgrowth of the dorsal arches (GOEPPERT's "Rippentraeger"). The osseous transverse process of the adult is a somewhat complicated structure, because it is composed first of this

increase in size and length towards the tail, where they gradually pass into the well-known ventral arches, which meet and fuse below the aorta.

Still more primitive conditions he found in a larva of *Menobranchus lateralis*, of only 22 millims. in length. The ventral arcua lie in the same transverse level with the neural arches, extend horizontally, and neither meet each other below, nor the neural arches on the lateral side of the chorda. In the anterior trunk-vertebrae of the same larva, the ventral basalia do however meet the neural arches. Lastly, in the tail, these ventral basalia are bifurcated, sending out a lateral process, which eventually carries the capitular or primary basal portion of the rib, and a vertical downward process, which, with its fellow of the other side, tends to enclose the caudal artery and vein. GOEPPERT has herewith shown the very close resemblance between the Urodela and the Selachians, Dipnoi, and cartilaginous Ganoids.

cartilaginous dorso-lateral process; secondly, of a broad string of connective tissue which extends out of the lateral mass of the skeletogenous layer to the capitular portion of the rib, and which represents part of the lost cartilaginous basiventral element. In the triangular space, enclosed between this string, the chorda, and

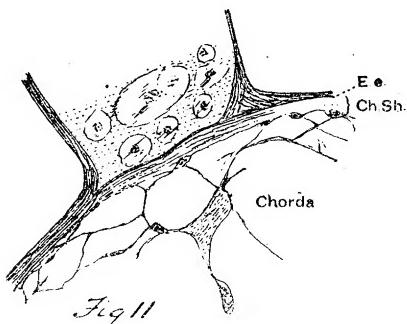


Fig. 11

Portion of a transverse section in level of the base of a neural arch (intravertebral) of a larva of *Salamandra*. Same magnifying power as that of fig. 10.

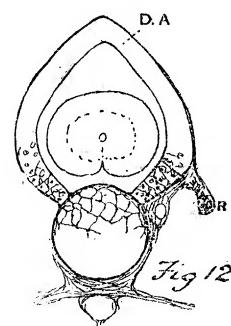


Fig. 12

Transverse section of the trunk through the level of the neural arches of the same larva.

the "Rippentraeger," lies the vertebral artery. The "transverse processes" of the tail are composed entirely of such ossified connective tissue, and are not preformed in cartilage; they would carry the ribs, if there were any in the intermuscular transverse septa of the tail.

The spinal nerves issue, throughout the vertebral column, immediately behind the bases of the neural arches, basidorsalia; their exits lie, in the adult, far in front

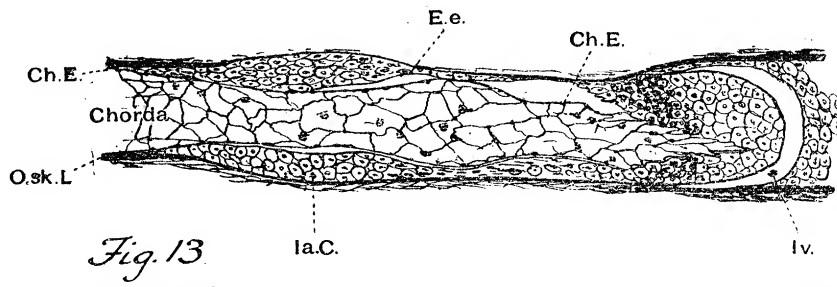


Fig. 13

Sagittal section through the axial portion of the vertebral column of a larva of *Salamandra*.

Ch.E. = Chordal epithelium.

E.e. = Elastica externa.

Ia.C. = Intravertebral cartilage.

IV. = Intervertebral joint cavity.

O.sk.L. = Outer skeletogenous layer.

of the intervertebral joints. This intravertebral position of the nerve is, of course, primarily caused by the nerve issuing between the basidorsal and the interdorsal of its vertebra, but it is emphasised by the subsequent great head- and tailward expansion of the intravertebral mass of the vertebra; the bony mantle, namely, which extends from the arches back- and forwards over the intervertebral cartilaginous

ring, causes the latter to establish its fullest development further and further away from the middle of the primitive vertebra.

One of the last changes of importance is the appearance of intravertebral cartilage, which, starting in level of the arches in the shape of a ring between the *Elastica externa* and the *membrana reunions*, first causes a thickening of the skeletogenous layer towards the *chorda*, and then gradually constricts the latter. Frequently this cartilage remains in ring-shape, and the *Elastica externa* as well as the chordal epithelium remain intact. But there are many cases in which this annular ingrowth of multiplying cartilaginous cells is so rapid that it causes ruptures in the chordal sheath, so that cartilage cells actually find their way into the meshwork of the *chorda* itself. Ultimately the *chorda*, in level of the arches, may be destroyed completely, its place being taken by a cartilaginous septum. Such conditions had misled GEGENBAUR (Lit., No. 51) to the assumption that chordal cells turned into cartilage.

GEGENBAUR described, and figured, this "chordal cartilage" in *Cæcilia*, *Menobranchus*, *Siredon*, *Menopoma*, *Salamandra*, *Triton*. STÖHR (Lit., No. 89) figured it clearly in the cervical region of the 30 millims. larva of *Triton cristatus*; FRAISSE (Lit., No. 44) gave an excellent figure of it in an adult *Pleurodeles Wattli*. Quite recently FIELD (Lit., No. 42) described and figured it as "Intrachordal-Knorpel" in *Amphiuma*. In *Anura* it is only GOETTE (Lit., No. 54, p. 395–397, 387–389) who mentioned chordal cartilage, giving a somewhat incoherent account of conversion of the *chorda* into cartilage. This "chordal, intravertebral, or intrachordal" cartilage has been almost completely ignored in the various text-books. (WIEDERSHEIM, 'Grundriss d. vergl. Anatomie' (1893), p. 61, fig. 41, has marked it CK., which was intended undoubtedly for Chordal-Knorpel, but he calls it "intervertebrale Knorpel und Fettzellen.") Perhaps one of the reasons of this neglect is that this cartilage is rather late and somewhat erratic in its occurrence. I myself have found no trace of it in about 600 consecutive sections through the posterior half of the trunk of *Salamandra maculosa*, a specimen just metamorphosed; nor did I find any in the tail and posterior trunk of nearly adult *Triton cristatus*. GEGENBAUR saw it in larvae of *T. cristatus*, but not in those of *T. tæniatus*. The fact is, that this cartilage appears first in the cervical region, and proceeds towards the tail, which it may, however, never reach. It is present in the whole trunk of probably all fully adult *Urodea*, but morphological investigations, being by predilection restricted to sections of limited portions of embryos and larvae, fail in many cases to reveal what is disclosed by comparison of older specimens and of several species.

LVOFF (Lit., No. 69, 1887, p. 462) was the first positively to contradict the supposed chordal origin of this cartilage. "Der Knorpel, welcher sich in der Chorda befindet (Axolotl), wird nicht, wie GEGENBAUR und GOETTE meinen, von Elementen der Chorda gebildet, sondern wächst aus dem Perichordalgewebe (skeletogenous layer) hinein und zerstört die Chorda in der Vertebralregion, indem er sie hier einschnürt. Auf der Chorda-Oberfläche befinden sich Chorda-Epithelzellen." Invasion of the chordal sheath

by cartilage cells through the Elastica externa was likewise clearly described by him in Elasmobranchi and Dipnoi; see also his fig. 25, Plate 6, of *Protopterus*.*

ZYKOFF (Lit., No. 93) has corroborated and slightly corrected LvOFF's conclusions, so far as Amphibia are concerned. He observed in the very young larva of *Siredon pisciformis*, of only 37 millims. in length, that the chordal sheath in the middle of the vertebra, *i.e.*, in the region of the arches, is reduced to a single lamella (the Elastica externa); that cartilaginous cells from the intervertebral ring creep into the intravertebral region and there form the intravertebral ring, or septum, in the adult; that these cartilage cells lie originally in exactly the same level or stratum as the intervertebral cartilage, namely, immediately outside the Elastica externa, which latter is ultimately ruptured, with the result that the chorda is partly filled with immigrating cartilage cells.

It is of little importance whether this "chordal cartilage" is derived from the intervertebral cells (ZYKOFF) or from the bases of the arches. Anyhow, by its position, inward growth, and occasional perforation of the Elastica externa, it bears great resemblance to the formation of the chorda-centra of Selachians and Dipnoi. But there is this difference, that in these fishes the chordal sheath is already very thick before it is filled by the invading cartilage, while in the Amphibia, in level of the arches, the chordal sheath is practically absent, being reduced to the E. externa, and cannot, therefore, be invaded. Whatever cells break through the E. externa find themselves at once in touch with the chordal epithelium, eventually within the chorda itself. If we assumed, for argument's sake, that the Urodela possessed a thick chordal sheath (Elastica interna and externa), the intravertebral portion of their vertebræ would undoubtedly be made up of chorda-centra. However, it would be pedantic to class the Urodela with the chorda-centrous Elasmobranchs, Holocephali and Dipnoi, although, when an intravertebral cartilaginous septum is completed, this portion of the vertebral body is practically a chorda-centrum. Consequently, the Urodela are obviously derived from a Dipnoid stock, a gradual diminution of the intravertebral axial cartilage being traceable from Perennibranchiata to Caducibranchiata. In the former, this cartilage does not only assume greater dimensions, but it also appears much earlier in the larva, while in Newts and Salamanders it is delayed and much restricted. In this respect the Amphibia represent a collateral branch to the osseous Ganoids, both being referable to a Gano-Dipnoid ancestral stock.

On the Atlas of the Amphibia, and on the so-called Proatlas.

The atlas of the Urodela possesses an odontoid-like process. W. K. PARKER ('Skull of Urodelous Amph.', p. 572) stated correctly that this process was formed by a pair of cartilages, PARKER's posterior parachordals, and these are, of course, serially homologous with the ventral arcualia in the *bond fide* postcranial region.

* I regret having neglected to state this case of priority in 'Phil. Trans.,' B, 1895, but KLAATSCH ('Morph. Jahrb.,' 1893) has referred to LvOFF's discovery.

This odontoid-like process belongs to a skleromere, the rest of which, namely dorsal arcualia, has been added to the occipital part of the cranium (*cf.* STÖHR for Urodela, FRORIEP for Aves and Mammalia, ROSENBERG for Elasmobranchs, SAGEMEHL and GEGENBAUR for Ganoids and Teleostei).

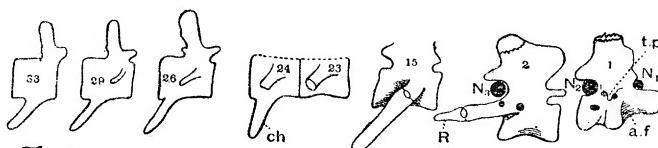


FIG. 14.

Oryctobranchus japonicus, adult; Cambridge Museum. The 1st, 2nd, 15th (trunk), 23rd (= 1st postsacral or caudal), 24th, 26th, 29th, and 33rd vertebrae.

The 24th vertebra, = 2nd caudal, is the first which possesses a perforated or paired ventral chevron; the 29th or 7th caudal carries the last distinct lateral process.

af in the first vertebra, is the articular facet for the skull; the body of the vertebra is perforated by three vascular foramina, between two of which projects a small ribless transverse process, *tp.* *N₁* = first spinal or suboccipital nerve.

The base of the transverse process of the 2nd vertebra is perforated by two vascular foramina. *R* = Rib.

The spinal nerve which belongs to this skleromere issues now immediately behind the occiput, above the odontoid-like process, and in front of the atlas. This is still the case in Urodela and in *Bufo vulgaris*, and in Gymnophiona, according to PETER (Lit., No. 79, p. 570), but in Rana, and many other Anura, this *N. sub-occipitalis*, s. *N. spinalis I.*, s. *N. proalanticus* (ALBRECHT) is lost; consequently the first of the nerves actually existing in the Frog is homologous with the second spinal nerve of Urodela and of Bufo. Moreover, since in all Amphibia and Amniota each spinal nerve lies *intravertebrally*, *i.e.*, issues behind the dorsal arch of its vertebra, it follows that, owing to the obliteration of a foremost skleromere (by its addition to the cranium), there are *n* vertebrae, but *n* + 1 spinal nerves, except in the Frog, and the 8th cervical nerve belongs to the 7th vertebra.

Again, the Amphibia possess no *N. hypoglossus*, at least not an intracranial XIIth pair of nerves, but in the Amniota at least two neuromeres and skleromeres have been added to the cranium, the first two postcranial spinal nerves of the Amphibia being converted into the Hypoglossus of the Amniota (*cf.* FRORIEP, GEGENBAUR).

Consequently, neither the "atlas" nor the second vertebra of the Amphibia is strictly homologous with the atlas of the Amniota; again, since "atlas" is the unalterable name of the first cervical vertebra of Man and the other Amniota, the second and first hypoglossal vertebrae of the Amphibia are *proatlantic vertebrae*.

It would not be necessary to dilate upon these facts and obvious conclusions if ALBRECHT had not perverted them, and if he were not followed by a considerable number of adherents, for instance, HOFFMANN, WIEDERSHEIM, DOLLO, BAUR, HOWES.

It is ALBRECHT's merit to have pointed out that "der *n* Spinalnerv eines amnioten Wirbelthieres durch den *n* - 1^{ten} Wirbel desselben austritt (Lit., No. 3, p. 453)."

He argues: If we put $n = 1$, then the first spinal nerve of the Amniota passes through vertebra 1 — 1, or 0. This 0th vertebra, to which belongs *N. spinalis I.*, must have been situated between the atlas and the occipitale, and may be called the *Proatlas*.

On p. 475 (Lit. No. 3), "Die Amphibien besitzen keinen zwischen dem Occipitale und dem ersten Halswirbel austretenden Nerven; der *N. spinalis I.* desselben tritt durch den Atlas." Here ALBRECHT, and many others with him, are wrong, because they took the highly modified Rana as typical of the Amphibia. "Bei den Amphibien tritt somit der n Spinalnerv durch den N. Wirbel, bei den Amnioten hingegen tritt der n Spinalnerv durch den $n - 1$ Wirbel." "Mithin ist der sogenannte Atlas der Amphibien dem Atlas der Amnioten nicht homolog, sondern dem Proatlas derselben homolog. Und mithin ist überhaupt der sogenannte Atlas der Amphibien in Wirklichkeit der Proatlas derselben." ALBRECHT has consequently arrived at a right conclusion, although one of his premises is wrong, namely the supposed non-existence of the suboccipital nerve in Amphibia.

ALBRECHT thought, moreover, that he had found remnants of the proatlas in the Amniota, in the shape of the free dorsal piece on the top of the atlas of Crocodiles, of Hatteria and even of Erinaceus. He called this paired, or unpaired piece, the eparcuale proatlantis. A little consideration shows that this piece is the neural spine (eparcualia in BRÜHL's and ALBRECHT's nomenclature) of the atlas itself, not of the proatlas, which latter we know to have joined the cranium. It is surprising that not one of ALBRECHT's school has seen this fallacy, all the more because ALBRECHT had laid stress upon the fact that the whole neurapophysis consists originally of a hyparcuale (my basidorsal proper) and of an eparcuale (my supradorsal), while, in addition to these, there occur spinal epiphyses even in Reptiles (*cf.* Lit. No. 9).

If the piece in question were the eparcuale of the proatlas, the atlas itself would be devoid of its eparcuale. Proper dissection of the *N. suboccipitalis* in Crocodiles shows that it issues and is distributed in front of the atlas and its top-piece. ALBRECHT himself had begged the question by looking upon the imperfect facets of attachment of the dorsal piece to the atlas as those of a zygapophysial joint.

In Hatteria the two pieces of the "proatlas" "articulate upon the skull" (HOWES, Lit. 62), but to consider this connexion a primitive feature with any bearing upon the morphological value of these pieces, is a conception which might almost endanger the probability of their being pieces of a vertebra at all.

Since the above account has been written, I have received Dr. PETERS' paper (Lit. No. 79), through the courtesy of the author, but I need not here discuss this Freiburg paper.

Summary of Important Features of the Urodela.

- I. The presence of four pairs of cartilaginous elements in each vertebra. These are :—

1. A pair of basidorsalia which form the neural arch.
 2. A pair of basiventralia which produce
 - a. Lateral outgrowths which become the ribs.
 - b. Ventral outgrowths, or hæmapophyses in the tail, where they enclose the caudal vessels.
 3. A pair of interdorsalia } which, at an early stage, form a broad ring
 4. A pair of interventralia } of intervertebral cartilage.
- II. The basidorsalia and basiventralia fuse together and form the body of the vertebra, the fusion being effected chiefly by the calcification and ossification of the lateral connecting portion of the skeletogenous layer.
- When, as in the trunk, the basiventralia are reduced or suppressed, the body of the vertebra is formed by the neural arch and by the ossifying skeletogenous layer only. This intravertebral bone-belt is also a feature of *Amia* and *Lepidosteus*.
- III. The production of hæmal outgrowths of the basiventralia, forming caudal, sub-vertebral canals, is also met with in *Amia*, in *Dipnoi*, cartilaginous Ganoids, and even in many Selachians, e.g., in *Alopecias vulpes*.
- IV. The intervertebral mass of cartilage either remains united, or opisthocœlous joints are formed within and across this cartilage, apparently in the same way as in *Lepidosteus*.
- V. The ribs start originally with capitula, which are at first continuous with, and then form joints with the lateral processes of the basiventralia; when these are reduced, the ribs retain only their tubercular attachment, which they have gained by forming connections with dorsi-lateral outgrowths, or diapophyses, of the neural arches.
- VI. The basidorsalia do not carry separate supradorsalia, nor dorso-spinal elements. The absence of such separate elements (and the same applies to the ventral side) constitutes the only absolute difference between Amphibia and Fishes.
- VII. The vertebræ do not possess, and cannot form, neuro-central sutures, because their bodies are exquisitely arco-centrous, formed, in fact, by the arches proper, namely, by the basidorsalia and basiventralia, while the interbasalia produce the neutral, intervertebral mass. Hereby the Amphibia differ from the Amniota. *I, therefore, distinguish the Urodele vertebral bodies as Pseudocentra.** The terms Pre- and Postcentra, as used in *Amia* and in certain Jurassic Ganoids, are not applicable to Amphibia.†

* The caudal vertebræ might be called Holocentrous, because their bodies, taking the central mass from joint to joint, contain all the four pieces of arcualia fused together; or they might be called Mesocentrous, with regard to the median position of the arches with the interarcual cartilage at either end. But these terms would not express the leading differences between Urodela and the other Tetrapoda so well as "Pseudocentra," especially if certain fossil Amphibia and Reptilia come into consideration.

† A suggestion had been made by myself ('Phil. Trans.', B, 1895, p. 193, last paragraph), concerning

ANURA.

The cells of the chorda lose their nuclei and protoplasm during the early tadpole stages, but the peripheral "chordal epithelium" remains longer in existence. The chordal sheath is thin, cuticular, its bulk consists of a concentrically lamellar mass which is surrounded by a very thin, highly refracting elastic membrane. This Elastica externa persists as a complete unbroken ring. The skeletogenous layer makes its appearance at first in the right and left dorsal corners between the chordal sheath and the medulla, while laterally and ventrally the chordal sheath is surrounded by a thin membrana reuniens. Cartilage appears in the shape of dorsal arches which rest almost directly upon the elastica; their bases remain separate from each other for a considerable time. These arches grow upwards, enclosing perhaps more than half of the medullary canal, but they also extend head and tailwards into what will ultimately become the intervertebral region. This extension of cartilage leads to a fusion with that of the next following pair of arches, so that the primitive axial column now consists only of a right and a left longitudinal ridge of cartilage from which are sent off dorsal processes, namely, the arches, in metamic succession.

Next appears on the ventral side of the chorda, an unpaired, median mass of connective tissue, being of course a swelling of the skeletogenous layer, but still without any cartilage.

The next stage is characterized by the increase of the intervertebral cartilage in such a way that the cartilage immediately behind the bases of the dorsal arches grows rapidly inwards, and henceforth constricts the chorda by hindering its further growth. This ingrowth compresses the chorda in *Rana* laterally, but in *Bufo* the cartilage grows obliquely downwards and inwards. Consequently, transverse sections of the chorda of these two Amphibia will give different pictures. The ingrowth from above, or rather from the dorsolateral corners (in *Hyla* and *Bufo*) and immediately behind the dorsal arches (*basidorsalia*) is significant, because it enables

a certain mode of formation of the Amphibian and Amniotic centra, which might be connected with that which exists in certain Elasmobranchs. This suggestion is true to a limited extent only. The chordal sheath is too well developed in the early embryos of Urodela and the so-called chordal cartilage does not invade the chordal sheath.

The arch centra of the Tetrapoda, and those of osseous Ganoids and Teleosteans, are, therefore, homologous. The apparent close relationship between Dipnoi and Amphibia fosters, of course, the inclination to homologize the intravertebral ingrowth of the so-called chorda-cartilage with that cartilage which invades the chordal sheath of the Dipnoi. Possibly this process is essentially the same in the Tetrapoda, but with this difference, that in them the process is arrested, and stops short of a perforation of the Elastica externa, while the rest of the chordal sheath, the E. interna, is reduced to insignificance.

But it is doubtful if this assumption of such a lingering reminiscence of Dipnoid features will unravel the mystery of the origin of the Amphibia further than to show that they have branched off from the Gano-Dipnoid stock.

us to recognise in it the interdorsal cartilaginous elements. The exit of the spinal nerves lies behind the arch, intravertebrally.

Ventral cartilaginous elements, comparable with basiventralia and interventralia, are rather tardy in making their appearance. At first they are indicated by the unpaired median swelling of the skeletogenous layer, which thickening is continued along the ventral side of the chorda. It is, of course, connected with the dorsal system of arcualia by a thin membrana reuniens. There is no clear indication that this ventral mass is composed of a right and left half. Cartilage appears in it in the shape of a similarly unpaired swelling; it becomes more bulky and somewhat semilunar in level of the dorsal arches, while behind them, in level of the interdorsalia, it grows less rapidly and restricts itself to the formation of a thin semi-ring.

This ventral cartilage never keeps step with the dorsal, the latter soon becoming preponderant. The cartilage of the dorsal arches does not join that of the ventral side, but both dorsal and ventral skleral portions become joined together and form the "vertebral" portion of the vertebra owing to the calcification and ossification of the skeletogenous layer so far as this is not cartilaginous. The resulting calcified ring protects the constricted chorda until long after the larval stage; in Rana, this intravertebral remnant of the chorda persists frequently throughout life, but in the adult Bufo and Hyla it vanishes, and is replaced by calcified, and partly by bony tissue.

The dorsal arches produce the zygapophyses and the long transverse extensions which carry the rudimentary ribs.

So far, then, is accomplished what some anatomists speak of as the "primitive Wirbel." Hereto is to be added the intervertebral mass.

In the Anura, the pair of interdorsal cartilaginous masses grows to much larger dimensions than the corresponding ventral mass, indeed so much that they ultimately almost completely surround and obliterate the whole chorda, first the chorda itself, lastly its sheath. The ventral cartilaginous mass (Hypo-chordal cartilage of some authors) takes a very small share in this process. Ossification of the non-cartilaginous remainder of the skeletogenous layer binds the whole structure together. The transverse, intervertebral joint appears closely in front of the dorsal arches; the spinal nerves issue immediately behind them. The so-called intervertebral mass remains with, and is added to, the caudal end of the vertebra; by far the greater share of the intervertebral mass falls to the interdorsal elements, including the articulating knob of these procoelous vertebrae.

The account given above is typical of the development of the axial skeleton of the trunk of Rana and Bufo. GEGENBAUR has named it "*perichordal*" in opposition to the "*epichordal*" mode which prevails in Bombinator, Pelobates, Pipa.

While, namely in the perichordal mode, the greater share of the formation of the

whole vertebra falls already to the dorsal cartilaginous elements, the epichordal type shows an almost complete suppression of both basiventral and interventral elements, so that the chorda remains for a long time on the ventral surface of the vertebral column in the shape of a flattened longitudinal band. These two types are, however, not unconnected. On the contrary, the suppression of the ventral elements is one of degree, not only in the various genera of Anura, but also in the same individual. It applies most typically to the trunk region, while "hypochordal" cartilage exists in the anterior cervical vertebrae, and, above all, in the coccygeum.

GEGENBAUR has already pointed out that these two modes of vertebral development are of taxonomic importance. It is at least most significant that the epichordal type coincides with a rudimentary tympanic cavity, namely, in *Pipa*, *Pelobates fuscus*, *P. cultripes*, *Bombinator*, and by inference, probably in *Alytes* and *Xenopus*. Moreover, *Pseudis* seems to take an intermediate position, because GEGENBAUR found in its young larva a considerable amount of hypochordal cartilage, while J. MUELLER stated its absence in older specimens. *Pseudis* is classed with the Cystignathidae, a family in which the state of reduction of the tympanic cavity is very variable.

However, until a much greater number of anurous genera have been examined, it will be enough to point out that the genera with epichordal development are *not* the lowest of the recent Anura, but their most specialised members. The epichordal type of their trunk vertebrae represents the terminus of one line of development which it is not difficult to connect with that of the Archegosauri.

It would be interesting to study the development of *Pipa* and of *Xenopus* more scientifically than has been done hitherto. These creatures are pre-eminently aquatic and probably their opisthocelous (or amphicelous?) vertebrae will show also a reduction of the interdorsal cartilage.

The *os coccygeum* has retained more primitive conditions in so far as much dorsal and ventral cartilage is developed in the skeletogenous layer. On the other hand, this cartilage is further advanced than in the trunk, because it has lost almost entirely its metamerie arrangement, and the posterior half of the coccygeum is formed chiefly by the ventral mass of cartilage, while the dorsal elements are more and more reduced. Only two vertebrae, generally the 10th and 11th of the whole series, are clearly visible, each being composed of a pair of dorsal and a pair of ventral cartilaginous blocks. Further back, cartilage extends tailwards in the shape of two dorsal and one ventral longitudinal bands or rods, which at first are separate from each other, but soon meet and fuse. Dorsally, the cartilage surrounds the spinal chord; the latter degenerates towards the end of the larval period, leaving, however, the spinal canal. The chorda, completely surrounded by cartilage, persists into the postlarval stage, but is destroyed long before the creature attains maturity. Ultimately the coccygeum receives a mantle of bone, owing to calcification and ossification of the outer portions of the skeletogenous layer.

GEGENBAUR concluded correctly that the coccygeum is equivalent to a whole

group of vertebræ, but he abstained from stating their number. It is, however, possible to approach this question analytically.

In *Bombinator*, according to GOETTE's figures, the 9th vertebra is the chief supporter of the ilium; the 10th vertebra is free, but occasionally (*cf.* GOETTE, fig. 346) sends out a weaker transverse process, long enough to reach the ilium. This amounts to a shortening of the trunk by headward migration of the pelvis (*cf.* the study of the analogous feature in Birds and Mammals by FUERBRINGER, GADOW, RUGE). The 11th vertebra is free during the larval stage only, but it soon fuses with the 12th, which is at no time completely separable from the coccygeal mass proper.

In the young *Bombinator*, just after its metamorphosis, there are at least fourteen spinal nerves, indicating that at least four vertebræ, including the 11th, have entered into the formation of the coccygeum. The 14th nerve-exit lies in level of the anus. For some time the coccygeum extends still further back and shows (*cf.* GOETTE, fig. 343) about nine irregular transverse constrictions. The same stage shows in all about twenty-two myomeres, about eight of which correspond with the postanal portion of the coccygeum. It seems, therefore, probable that the whole coccygeum contains the cartilage of about twelve skleromeres.

The whole postsacral portion of the axial skeleton of the Anura bears a great resemblance to the posterior portion of the caudal axial skeleton of Dipnoi and of Chimæra, in so far as both chorda and spinal cord disappear and the cartilaginous elements are fused into a continuous rod.

The Tail, namely, that portion which is absorbed during the metamorphosis of the Tadpole into the anurous Amphibian. The tail remains throughout its existence in an apparently primitive condition, resembling that of a Lamprey's larva before the appearance of cartilage. The chorda is a thick rod; its outer cells form a clearly visible layer of so-called chordal epithelium. The chordal sheath is thin, about one-fifth of the thickness of the whole chorda, externally surrounded by a well-marked unbroken Elastica externa, which in transverse sections shows numerous undulations produced by shrinkage. A mass of connective tissue, triangular in transverse sections, rests dorsally and ventrally upon the elastica; it surrounds the spinal canal and the ventral median blood-vessels. The apices of these triangular masses extend into the dorsal and ventral caudal fins. Excepting the intermuscular septa there is nowhere any indication of metamerism in the skeletogenous layer. The spinal cord, although smaller than in the coccygeal and trunk regions, extends nearly to the end of the tail.* Cartilage is, and remains, entirely absent.

Both spinal cord and chorda undergo a process of degeneration during the meta-

* In the larva of *Hyla septentrionalis* the neural mantle of the spinal cord disappears gradually towards the end of the tail, but the central canal extends further, and is surrounded by its peculiar cellular tissue. The chorda dorsalis is still large.

morphosis; the reduction begins at the end of the tail and keeps step with the disappearance of the whole organ.

For some unaccountable reason there seems to have been started the notion that the Tadpole's tail is not a phylogenetic, ancestral organ, but that it owes its existence to adaptation to the aquatic life of the larva. Certainly the aquatic life keeps the tail functional and preserves it for some time, but it is present, nevertheless, in the embryo of *Hylodes martinicensis*, which undergoes its metamorphosis within the egg. The presence of a chorda dorsalis and spinal cord in the tail of the anurous Amphibia, and the fact that the tail is constructed exactly like the anterior portion of the axial column, demonstrate the untenability of the notion mentioned above. The Tadpole's tail represents a typical vertebral column before the appearance of cartilage. Strictly speaking, the tail begins with the first or second postsacral vertebra. That portion of the whole tail shows the strongest development of cartilage, with subsequent loss of metamerism, and becomes the coccygeum, which is required to form a "backbone" for the enormous belly of the *Anura*, perhaps because of the great shortening of the trunk proper. The rest of the tail has during the phylogenetic development of these Amphibia gradually lost its segmental nature and its cartilaginous elements; it looks now during its ephemeral existence like a pseudoprimitive organ.

An analogous case to the stowing away of a considerable portion of the alimentary canal in, or rather below, the tail, is afforded by many Tortoises, in which a portion of the rectum, and, of course, the cloaca, with its derivatives, is retained in the caudal region.

Summary concerning Anura.

The salient feature is the preponderance of the dorsal cartilaginous elements over their ventral counterparts.

The gradual suppression of the pair of interventral cartilages is compensated by the stronger development of the interdorsalia.

Basidorsalia and basiventralia fuse together by direct ossification and calcification of the connective tissue. This fused mass is homologous with that of the Urodela, but forms, in Anura, the cranial half of the vertebra, perhaps owing to the formation of opisthocœlous joints.

The caudal portion is, in the trunk, formed entirely by the interdorsalia, and when these two fuse into one compact mass they establish a true centrum, comparable by its place, but not by its composition, with the postcentrum of Amia. This centrum of the Anura, being genetically the united interdorsalia, may be termed *noto-centrum*.

The ribs are much reduced in size, and are carried entirely by the neural arches. Those embryologists, whose belief in the absolute truthfulness of the ontogenetic recapitulation is not curbed by the study of comparative anatomy, do

not fail to consider these ribs of the Anura as non-homologous with those of the Amniota.

Comparison of Anura with certain Palaeozoic and Mesozoic Amphibia and Reptilia.

The vertebræ characteristic of recent Anura consist, as we have seen, of three pairs of arcualia, or if, of these, the basiventrals be lost, they consist of the two pairs of dorsal arcualia only, *e.g.*, in *Pipa*, *Bombinator*. It is of the utmost interest that this treble composition, by three pairs of elements, which are not fused or co-ossified, as is the case in recent Anura, prevailed throughout life in the vertebræ of many palæozoic Amphibia. This condition has been termed *rhachitomous* by COPE. The basiventrals are fused into one strong crescent, which lies ventrally below the neural arch; this ventral crescent is the *Hypocentrum* of GAUDRY. In the tail it possesses large hæmapophyses which enclose the caudal canal. The interdorsalia form a pair of wedges behind the neural arch; these dorsal wedges are not united above the chorda, they ossify later than the basiventral crescent, and have been called *Pleurocentra* by GAUDRY, who most correctly considered that the body, or rather the axial part of such a vertebra, was composed of a Hypocentrum and two Pleurocentra.

Such three-partite vertebræ with interdorsalia, basidorsalia, and basiventrals, are those in the trunk of *Archegosaurus*, *Euchirosaurus*, *Actinodon*, *Sparagmites* (?) and of what is supposed to be a young specimen of *Mastodonsaurus*.*

The phylogenetic stage, which must have existed previously to this three-pieced type of vertebra, must have contained all four pairs of arcualia, namely, in addition, the pair of interventralia, which in the larvæ of Anura we saw to be in the process of reduction. Such four-pieced vertebræ are actually known.† The interventralia are mainly represented by a pair of small separate cartilages, or bones, which lie below the interdorsalia, for instance, in the tail of *Archegosaurus*, in *Chelydosaurus*,

* There is no evidence, whatever, that the three little segments, exquisitely three-partite, figured by v. MEYER (Lit., 74, Plate 7, figs. 5 and 6), and by v. ZITTEL (Lit., 91, p. 407, fig. 403), belong to a young *Mastodonsaurus*. v. MEYER, on p. 67 of his work, has only made a very reserved suggestion. And still this specimen has been used by others as a proof that fusion of the three pieces produce the solid, stereospondylous, vertebræ of *Mastodonsaurus* and other Labyrinthodonts.

† It is to be borne in mind that, although there is no doubt about the homologies of these four pieces or elements, their relative positions are subject to much uncertainty. We know, as a fact, that in the Amniota the so-called wedge-bones become attached to, and often fuse with, vertebræ to which they do not belong genetically; we know, also, that the Odontoid forms one physiological unit with the second vertebra, and we know that the first trochoid joint (see 'Aves,' p. 45) is by no means always the same morphological quantity. Ribs migrate not only on to other processes, but even on to the "wrong" segments; the dorsi-spinal muscles have carried these changes to the extreme. In short, the principle of metamerism still prevails, but the primary particularistic feature of such skleral fractions as the ribs, namely, to remain with their own particular skleromeres, with due regard also to the myomeres, is now often suppressed by practical adaptation to new function and requirements. It is the use to which an organ is put which models its shape.

and in *Sphenosaurus*. FRITSCH, who discovered them in *Chelydosaurus*, named them hypocentralia pleuralia, and most happily compared them and the pleurocentra with the intercalaria (*i.e.*, interventralia and interdorsalia) of cartilaginous Ganoids.

It is conceivable that the pleurocentra or interdorsalia, which genetically belong to a certain vertebral complex, are those which lie in front of the big neural arches, and that the interventrals of the same serial number are those which lie behind the basiventralia, or *vice versa*. This cannot always be decided in fossils. Sometimes the triangular bases of the neural arches sink in between the hypo- and the pleurocentrum. GAUDRY restores the vertebræ of *Archegosaurus* in a way which is opposed to that preferred by FRITSCH, and still the chief result is the same. In a good number of fossils these three or four pairs of semi-rings, arches, and other pieces remind us of the blocks of certain puzzles, especially when only the bony parts, or the cartilage, is fossilized, while the connecting matrix is lost.

Archegosaurus and *Sphenosaurus*. I agree with FRITSCH that the basalia form the front part, the small interbasalia the posterior portion of the whole vertebra. The basiventralia (hypocentrum arcuale) have the greatest share in the formation of the "body." In *Sphenosaurus* they carry the ribs of the postthoracic region. In *Archegosaurus* the ribs have lost their capitula and form very distinct tubercular facets upon the neural arches.

In *Chelydosaurus* the interventralia (FRITSCH's hypocentra pleuralia) are still double; in *Sphenosaurus* they are confluent, and form a ventral small semi-ring. Through this circumstance FRITSCH was misled to homologize them with the "intercentra" of the Amniota, a mistake very easy to make, considering the markedly intervertebral position of these elements in *Chelydosaurus*.

Trimerorhachis. The vertebræ of the trunk are composed of large basidorsalia, basiventralia, and a pair of large interdorsals, which latter lie behind the neural arch and form broad articular facets with the cranial margin of the basiventral mass next behind. When COPE, in the original figures lettered the basiventralia (hypocentra arcualia of FRITSCH and GAUDRY) *i*, indicating intercentra, he was right in so far as these elements are homologous with the wedge-bones of the Amniota. But his real reason for calling them "intercentra" in *Trimerorhachis* was, that he considered the pleurocentra alone to constitute the centra. There is not much fault to find with his conception, because in those cases in which both the pleurocentra and the hypocentra arcualia are of equal size, both enter into the composition of the "body." If the hypocentrum arcuale (basiventral) is preponderant and carries the neural arch, the type of the Urodelous pseudocentra still prevails to a certain extent; on the other hand, the preponderance of the pleurocentra (interdorsalia) leads to the type of recent Anura.

Eryops (fig. 41, see p. 41). The neural arches of the tail and thorax rest exclusively upon the posterior disk (pleurocentra of COPE). In the thoracic vertebræ the diapophyses of the neural arches alone carry the single-headed ribs. In the cervicals, the

articular facet extends downwards and forms a shallow groove on the caudal portion of the "intercentrum" or basiventral. This is exactly what is the case in many recent Reptiles also.

Now, this posterior disk, or the paired wedges in the trunk, between the neural arch and the "hypocentrum" have been taken by COPE for the pleurocentra, owing to the assumption that these pieces of Eryops are the same as those of other "rhachitomous Stegocephali." But this is not the case. These elements of Eryops are ventralia, not dorsalia, consequently not pleurocentra. They are interventralia, enlarged and extending upwards. Consequently they are homologous with FRITSCH's hypocentra pleuralia of Chelydosaurus, of the tail of Archegosaurus, and homologous with the centra of the Amniota. They are, moreover, the piece which, in Eryops, is attached to the caudal end of the cervical vertebra, figured by COPE, and there actually and rightly called hypocentrum pleurale. These elements are not pleurocentra (interdorsalia) in Eryops. In COPE's drawing of this creature, some of the most ventral portions (visible between the lateral elements, which are promiscuously mentioned as *i* [intercentra] and as *ch* [chevrons]) are designated *p*, i.e., pleurocentra, but they are in reality interventralia.

The resemblance of the three-pieced vertebrae of Eryops with those of Archegosaurus appears to be great, but it is only superficial. The whole atlas of the Amniota is likewise absolutely rhachitomous, if by this term we understand that the rhachis, or shaft, or body, consists of several pieces, regardless of their individual homologies.

Now, it so happens that the very name Rhachitomus was the one first applied by COPE to the creature which he later on called Eryops; by law of priority, the term "rhachitomi" should therefore be restricted to those creatures in which the vertebrae contain basidorsalia, basiventralia, and interventralia (the latter becoming the centra), consequently to Eryops, and all recent *Amniota*, including, of course, all the *bona fide* fossil reptiles. The indifferent term for such vertebrae, which retain their component units in a separate unfused state, is "*temnospondylous*" (ZITTEL.)

The *embolomerous* type (COPE) is a further development of the rhachitomous type; the mass of interventralia grows upwards, and surrounds the chorda completely, being thus transformed into an archless disk, while the whole basiventral mass forms a similar disk, which carries the ribs, and in the tail throws out hæmapophyses, which enclose a caudal canal, while above it carries the neural arches. The latter are, however, not fused with the basiventral disk, and they have the tendency of shifting their bases upon the posterior disk. Such vertebrae bear a perplexing resemblance to the double caudal vertebrae of *Amia*, and still they have the same composition as the typical vertebrae of all recent *Amniota*. It is no wonder that the confusion in the synonymy of all these various pieces in Amphibia and Reptilia has become absolutely appalling.

And still, how is it that GAUDRY, FRITSCH, and COPE all differ from each other,

although every one of them discusses his own views with great clearness, and is generally correct in the interpretation of his own specimens? Simply because one began with Amphibia and the other with Reptiles; and they could not reconcile their respective views, because Amphibia and Reptiles do not form a continuous line of development, but are two divergent branches of a common stock of palaeozoic Tetrapoda with quadripartite vertebræ. The removal of Cricotus and Eryops from the Stegocephali (a most heterogeneous assembly, as has been pointed out by ZITTEL) to the Reptiles proper clears this difficulty to a great extent. But there are probably many creatures, whose systematic position is still obscure, and which have been placed wrongly; and, if evolution be true, there must have lived countless creatures with quadripartite vertebræ, which were a "rudis indigestaque moles," neither Amphibia nor Reptiles in the present intensified sense of the systematist.

The *Lepo-spondyli* (ZITTEL) afford another instance of a collective, heterogeneous group. Some of the lepo-spondylous creatures should be removed from stegocephalic to Gecko-Sphenodon-like relations. The thinness of the shell of the vertebræ can be a question of degree only; the main point is their composition. The Permian *Urocordylus* and *Keraterpeton* have typical Urodelous vertebræ (for figures see FRITSCH, fig. 80, p. 133, figs. 84-86). Longitudinal vertical sections show the chorda in various stages of compression, with even an intravertebral septum. The vertebræ of *Branchiosaurus* seem to have possessed no centra; they consist of two pairs of thin ossified pieces only, namely, a pair of basidorsalia and a pair of basiventralia, both meeting at a lateral suture, and contributing equally to the production of a transverse process, which carries the one-headed rib. The neural arches form a median dorsal, and the ventral pair forms a ventral median suture. These vertebræ are typically lepospondylous, so far as the ossified shell is concerned, but the cartilage we do not know.

Synonyms, concerning chiefly Amniota.

The first pair of basiventralia.

4^e pièce impaire, représentant le corps de l'atlas, CUVIER (he did not know the meaning of the odontoid).

Mittelstueck des Atlas (since RATHKE recognised as homologous with ventral arches).

Mittelstueck=vorderes Stueck des Atlaskoerpers, HOFFMANN (this idea has been adopted from J. MUELLER, Myxinoiden, p. 168).

Unterer Dornfortsatz oder erste Haemapophyse, JAEGER, 1858 (Birds).

Basilares Stueck, unteres Schluss-Stueck, azygos basilar or ventral piece, STANNIUS (Crocodile), HULKE.

Modificirter unterer Dornfortsatz, RATHKE (Snakes).

Hypapophysis, OWEN (Crocodiles); GUENTHER (Hatteria).

"Hypapophysial" segment of first centrum, FLOWER.

Inferior arch of atlas, FLOWER, etc.
 Arcus anterior, Haemalspangen, HASSE.
 Pseudocentre, hypapophyse entre l'occipital et l'atlas, ou arc ventral de l'atlas,
 ALBRECHT, DOLLO.
 Intercentrum I., COPE, BAUR.
 Erste hypochordale Spange (ventrales Schluss-Stueck des Atlas, FRORIEP).
 Postoccipital intercentrum, T. J. PARKER.
 Proatlanto---atlantic hypapophysis or intercentrum, BOULENGER.

The second pair of basiventralia.

Rechte und linke craniale Centroidal-Epiphysen des Epistropheus, ALBRECHT,
 1884.
 Zweite hypochordale Spange, FRORIEP.
 Hypochordal epiphysis of the epistropheus, MACALISTER (in Man).
 Postatlantal intercentrum, T. J. PARKER.

The third and following, cervical, basiventralia.

Hypapophysen oder untere Bogen der Halswirbel, HOFFMANN (not homologous
 with the chevrons of the tail).
 Ganz selbstaendige Fortsaetze des Wirbelkoerpers, GEGENBAUR (in Lizards not
 homologous with Crocodilian chevrons).
 Untere Dornen oder untere Dornfortsaetze, LEYDIG (in Lizards homologous
 with the lower arches in the tail).
 Lower or ventral arches, HUXLEY (homologous with the Crocodilian chevrons).
 Hypapophyses autogenes, ALBRECHT (in Hatteria).
 Hypapophyses, wedge-bones, OWEN, LEYDIG, HUXLEY, &c.
 Cervical hypapophyses, BOULENGER (homologous with chevrons).
 Intercentra, COPE, BAUR, DOLLO, ZITTEL.

The basiventralia in the tail.

Hypapophyses (the axial portion or disk), OWEN, HUXLEY, LEYDIG.
 Untere Bogen, lower or ventral arches (homologous with the intercentral wedges
 of the neck), LEYDIG, HUXLEY.
 Haemapophysen, oder untere Bogen der Schwanzwirbel, HOFFMANN.
 Arcus haemalis, HASSE.
 Gastrokyrtoma, BRÜHL.
 Intercentra = Zwischenwirbelbeine = os en chevron, chevron bones, sub-
 vertebral wedge bones, COPE, ZITTEL, DOLLO, &c.
 Haemapophyses (the chevrons proper), DOLLO.
 Intercentra (the axial portion, or disk, or the ventral crescents), DOLLO, BAUR.
 Untere Bogenstücke; aechte Haemapophysen, ZITTEL.

Hypocentra, GAUDRY.

Actinosts (the chevrons !), BAUR.

The first pair of basidorsalia.

Lateral pieces of the atlas. Seitenstuecke.

Dorsal upper half of the atlas. Arcus posterior. Neurapophysen.

Centrum I., in *Trimerorhachis*, COPE.

Pleurocentra, in *Actinodon*, GAUDRY, 1878.

The first pair of supradorsalia.

Lame transverse, CUVIER.

Dachfoermiges, oberes Schluss-Stueck, STANNIUS.

Dorsales Schluss-Stueck des Atlas, RATHKE.

Dorsales Schluss-Stueck des Bogentheiles (isolated spinous process), GEGENBAUR.

Neural spine of the atlas, OWEN.

Upper middle piece, sometimes double, of dermal origin, HUXLEY.

Dachstueck, Eparcuale (intercalated between occiput and atlas; double in embryos), BRÜHL, ZITTEL.

Rudiment eines verkümmerten Wirbels, BRUCH.

Eparcuale des Proatlas, ALBRECHT.

Eparcuaux droit et gauche du pro-atlas, DOLLO.

Pro-atlas, HOFFMANN, HOWES, BAUR, WIEDERSHEIM, ZITTEL.

Postoccipital bones, MARSH.

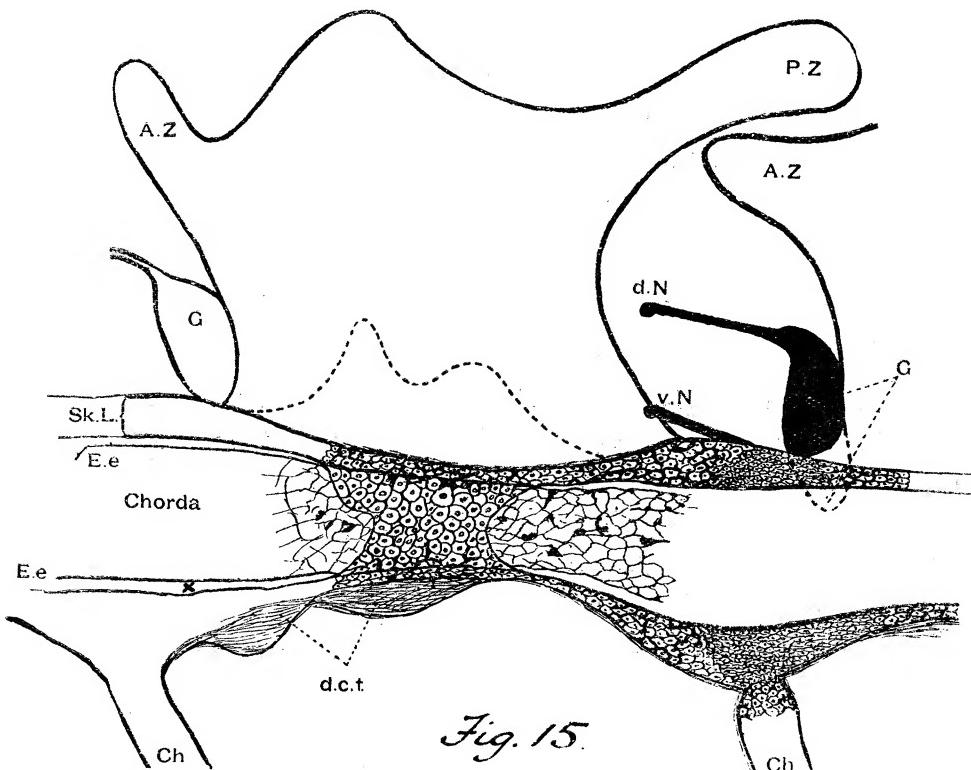
GECKONES. (Figs. 15 and 16.)

In addition to GEGENBAUR's description (Lit., No. 51, p. 49-52), I have examined the axial skeleton of several specimens of *Gecko verus*, and in consecutive sections the tails of *Hoplodactylus pacificus* and *Hemidactylus gleadovi*. There are several features in the gross anatomy of the Gecko's vertebral column, which are not generally known.*

Each vertebra consists of a pair of large neural arches, which rest with their broad bases upon the centrum. A neuro-central suture (indicated in my figure by a dotted line) remains throughout life, at least in the tail; in the trunk of old specimens this suture disappears externally.

* With the exception of a few short notes by STANNIUS, by HYRTL and GEGENBAUR, on the transverse division of caudal vertebræ, and by BAUR on the presence of intercentra, there are no original descriptions or figures published. It is, therefore, scarcely advisable to omit a more detailed account as superfluous, as has been done by WIEDERSHEIM (Lit., No. 91), who "glaubt eine ziemlich genaue Kenntniss der Skelet-Verhältnisse der Geckotiden voraussetzen zu dürfen."

Each centrum, the odontoid excepted, consists of a cartilaginous tube, more or less calcified and ossified, which, having a narrow waist in the middle, and widening head-and-tailwards, might be compared in shape with that of an hour-glass, if it were not for the dorsi-lateral wing-like expansions, which extend considerably upwards to the neural suture. Exactly in the middle of the vertebra the shell of the centrum forms a cartilaginous septum, wrongly called chordal cartilage. When this septum is com-



Sagittal section through the tail of an adult *Gecko (Hoplodactylus pacificus)*.

d.c.t = dense connective tissue.

d.N ; v.N = dorsal and ventral roots of spinal nerve.

E.e = Elastica externa.

G = spinal ganglion.

Sk.L = skeletogenous layer.

An asterisk (*) indicates the space which is due to shrinkage of the chorda and its sheath away from the skeletogenous layer.

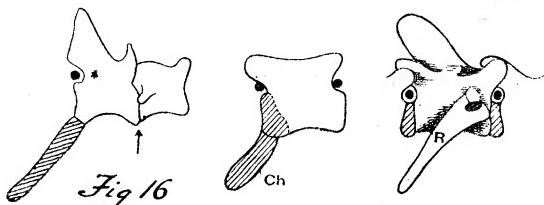
plete, and this seems to be the normal condition in the tail, the chorda is rent asunder; when, however, the septum is incomplete, for instance, in the trunk of *Phyllodactylus*, the chorda is only constricted, and is, consequently, continuous throughout the vertebral column, with the exception of the thin end of the tail, where, as in *Dipnoi*, *Urodela*, and many Lizards, the whole chorda is destroyed and replaced by cartilage.

This septum is only slightly invaded by ossification, and consists of large nucleated cells, which retain the appearance of young or embryonic cartilage. It coincides

exactly with the line of transverse division of most of the caudal vertebræ into an anterior and a posterior half.

Between the centra of every two successive vertebræ lies a separate element, the so-called intercentrum. It is broadest ventrally, of crescent or wedge-shape, and appears in macerated, sun-dried skeletons of lighter colour than the adjoining centra. In the dried skeleton they seem to consist only of ventral semi-rings, but in the fresh condition, and still better in consecutive sections, they reveal themselves as complete rings, which completely grasp round the chorda; the ventral third or half, namely, the crescent, is alone calcified, the rest of the ring remains cartilaginous. It extends head-and-tailwards into the concave ends of the adjoining centra; there is no discontinuity of the tissue, but the cells of the ring are much denser and more closely packed; they are not pervaded by ossification, except on the inner or chordal surface of the ring. The whole ring acts as an articular pad instead of a joint, there being no proper joints, nor is there any indication of joint-cavities.

The thickness of the rings varies much, not only in different genera, but even in the various regions of the same individual. They are either thin, not interfering with the chorda, which attains its widest diameter in this region, for instance, in *Phyllodactylus*, *Hemidactylus*, *Hoplodactylus*, *Gecko*; or, they are very thick and constrict the chorda considerably, as, for instance, in the trunk and tail of *Platydactylus*.



Gecko verus. Camb. Mus. One mid-caudal, one anterior caudal and one lumbar vertebra. The asterisk in the left figure indicates the place of origin, the ● the exit of the spinal nerve. The whole mid-caudal vertebra is divided into a smaller anterior, and a larger posterior portion, the former carrying the rudimentary transverse process, the latter the chevron. Basiventralia and chevrons are noted obliquely.

The first of these rings is, in so far, exceptional, as it forms the ventral half of the atlas ring. The second is attached to the cranial surface of the second centrum, and produces, like some of the next following ones, a vertical median ventral blade of bone. Between the thoracic, lumbar, sacral, and first three or four caudal vertebræ these "intercentra" possess no unpaired ventral outgrowths. In the tail they are enlarged, sometimes into thick triangular wedges. They carry moreover a pair of chevrons. These are preformed in cartilage, and incompletely separated off from the wedges or crescents; they have the tendency of fusing by superficial ossification, with their crescents, and these again fuse with—or at least become firmly attached to—the caudal ends of the centrum next in front.

The dorsal and ventral roots of the spinal nerves arise closely behind the neural arches, but the ganglia and their exits lie somewhat further back; in the tail in a transverse level even somewhat behind the bases of the chevrons. The ribs of the neck and trunk possess a well-marked capitulum and tuberculum. The capitula of the cervical and lumbar ribs are attached to very short knobs near the cranial end of the centra; those of the anterior cervicals touch, or even extend their facets upon, the caudal margin of the "intercentra." Those of the thoracic region are removed somewhat further tailwards, near the middle of the centra. The ribs of the tail are much reduced, and, if present, are carried by, and fused with, the ends of the large transverse processes, which seem to be produced entirely by extensions of the centra.

The more remarkable features of the Geckos are consequently the absence of axial joints and the persistence and lifelong growth of the chorda. In these respects they still agree with many Urodela and differ from the other Amniota. But the resemblance to Urodela goes no further, because in the Geckos the bulk of the vertebræ is formed by the neural arches and the centrum, while the chevron-bearing elements have lost their contact with the neural arches, take no share in the formation of the centra, and are reduced to what cannot but be called an intervertebral position. This expression is unfortunate, because it has given rise to the erroneous attempt of homologising these intervertebral, or better, intercentrally-placed disks (which actually do the duty of intervertebral joints) with the intervertebral cartilaginous mass of the Amphibia.

The Geckos or *Nyctisauria*, or *Ascalabotæ* retain many primitive features (axial skeleton, auditory ossicular chain, cutis), in addition to numerous special modifications (eye, cutis, adhesive toes, otocysts). These, together with the world-wide distribution of these creatures, which in spite of this dispersal and their great number of forms are all remarkably alike, suggest that the Geckos are not only a very independent but also a very old branch of reptiles.

Fossil Geckos seem to be however, unknown, but there is an extraordinary resemblance of certain fossils to the caudal vertebræ of Geckos. For instance, the so-called *Palæohatteria* from the lower Permian of Saxony. More remarkable are some of the so-called lepospondylous *Stegocephali*, e.g., *Hylonomus*, *Smilicerpeton*, *Sparodus*, *Hylerpeton* from the Coal-measures and Permian of Saxony and Nova Scotia. I do not say that all these creatures were Geckos, or their direct ancestors, but I contend that at least these forms of *Lepospondyli* are not Amphibia (as *Stegocephali* are supposed to be), but already well advanced Reptiles. Their broad neuro-central sutures, their large movable chevrons, and in the trunk, the little interventral wedges, stamp them as Reptiles; the deeply amphicœlous centra and concomitant large remnants of chorda fall, of course, into the lepospondylous category, but this should mean nothing more than that the bodies of the vertebrae are still thin shelled, while the chorda is still large.

LACERTILIA.

Some Important Features of the Vertebrae of Adult Lizards. (Figs. 17–23.)

Basi-ventrals, in the shape of osseous, unpaired, nodules or wedges, persist between most of the cervical vertebrae; they are absent in the thoracic and lumbar regions, and reappear in the tail, either as little wedges or as chevrons. The first of the whole series forms the ventral half of the ring of the atlas, with the neural half of which it is connected by suture. The second fuses mostly with the cranial end of the second, and with the caudal and ventral surface of the odontoid; frequently the fusion is incomplete, even in adult specimens, e.g., in *Hydrosaurus giganteus*. Or the wedges may completely merge into the epistropheal mass, without leaving any outward traces, e.g., *Cyclodus*. The third wedge-bone behaves very variably; either it remains with

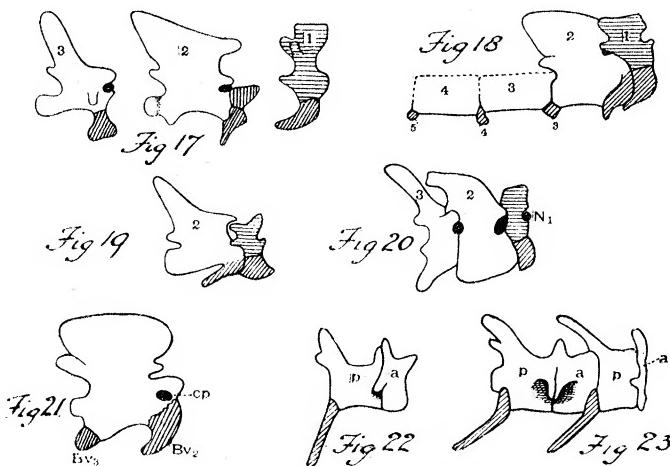


Fig. 17. *Iguana tuberculata*, adult. R. Coll. Surg., Lond. The first three cervical vertebrae.

Fig. 18. *Uromastyx spinipes*, adult. Camb. Mus. The first four cervical vertebrae and the first five basi-ventral elements.

Fig. 19. *Histicerus amboinensis*, adult. R. Coll. Surg., Lond. First and second cervical vertebrae.

Fig. 20. *Cyclodus gigas*, adult. Camb. Mus. First three cervical vertebrae.

Fig. 21. *Hydrosaurus giganteus*, adult. Camb. Mus. Second cervical vertebra, carrying the second and third basi-ventral elements. Cp. 2 = facet for the capitulum of the second rib.

Figs. 22 and 23. *Lacerta ocellata*, adult. Camb. Mus. Three complete caudal vertebrae, showing the natural division of each vertebra into a smaller anterior and a larger posterior portion.

the third vertebra, e.g., *Iguana*, or it attaches itself to the caudal corner of the epistropheus, so that the latter may eventually carry two wedge-bones, one at either end. The fourth and fifth vary; they remain interventral, retaining their independence (most Agamidæ, Iguanidæ, Lacertidæ, Scincidæ, and Chamæleonidæ), or they ankylose with one or other of the adjoining centra (Anguidæ, Varanidæ).

BOULENGER has found that there exists a peculiar correlation in this variable mode of attachment between the cervical wedges and the chevrons of the tail, which are,

of course, all serially homologous elements. When, namely, the cervical wedges remain independent, the same applies to the chevrons, and when the cervicals are attached to one centre, the same is found to be the case with the chevrons. He has, moreover, made the important observation that the anterior caudal wedges are sometimes paired, *e.g.*, *Heloderma*. When the caudal vertebræ are strongly procoelous, the knob is very long and the chevrons are attached to its neck, so that at first sight it is difficult to believe that they do not genetically belong to these vertebræ which carry them. This difficulty is somewhat increased by the further circumstance that the axial or central portion of these basi-ventrals has persisted as a sort of fibrous disc, which, even in older specimens, is interposed between the caudal end of the centrum and the articulating knob. The latter calcifies separately. In *Pseudopus* the chevrons are absolutely fused with the caudal ends of the centra, and consequently have a superficial resemblance to the vertebræ of *Urodela*.

The *Ribs* are perhaps best studied in well macerated and sun-dried skeletons of *Anguis*. In the trunk they possess thick capitula, which are attached to the cranial end of the vertebræ, near, or across the neuro-central suture; hooklike tubercula lie behind and slightly dorsally, without any direct bony attachment. In the tail the capitular portion is much reduced, while the tuberculum is much stronger, and lying behind (no longer above the capitulum) is directly fused with the body. A gradual change takes place in such a way that in the first double caudal vertebra the capitular portion remains as a fine bony thread with the anterior half of the centrum, while the thicker tubercular portion goes with the posterior half of the body. Further back in the tail the anterior half carries neither rib or transverse process, while the posterior half carries most of the neural arch and the rib, namely, the enlarged tubercular portion of the original whole rib. In the anterior caudals (they divide in *Anguis* from about the 6th or 7th onwards) the anterior portion is very narrow, scarcely one-sixth of that of the rest of the body; in the eleventh caudal the proportion is about 1 to 3 or 4. See also the drawings of the caudal vertebræ of *Lacerta ocellata*. Figs. 22 and 23, p. 29.

The general features of those dividing vertebræ (which are possessed by many families of the *Lacertilia*, also by the Geckos and by *Sphenodon*), have been fully described by HYRTL (Lit., No. 56) and by GEGENBAUR (Lit., No. 51). The latter pointed out that the split coincides in position with that of the intra-central septum of cartilage, that the split is not preformed in the embryo, but makes its appearance with the ossification of the vertebral bodies, and extends later into and across the neural arch and the various processes.

ÄLRECHT (Lit., No. 7) had the brilliant idea, propounded in the usual assertive style, that the break indicated the junction of the original proto-vertebræ (in conformity with the accepted notion of resegmentation), and that the line of division still retained inter-protovertebral tissue. Such tissue must be very primitive, non-

differentiated material and capable of producing almost anything of a skeletal nature, consequently it must easily be able to reproduce the lost half of its own vertebra.

Now then, this idea is really most suggestive. It would be considerably strengthened if it could be shown that the anterior or cranial division of such a vertebra were nothing less than the enlarged basiventral disk, which somehow met and fused with a pair of interdorsalia so as to enclose also the spinal cord. Then indeed the split would coincide with interprotovertebral tissue. But there is no support whatever for this speculation. On the contrary, all we can gather from the variations of these vertebræ, from the mode of formation and persistence of the cartilaginous septum, tends to show that these breaks are not reminiscences of pre-reptilian conditions, but are acquisitions. In Amphibia these vertebræ do not break off although there is a septum, but this coincides with the level of the dorsal and ventral basalia. The cartilaginous septum would, by extending into the peripheral portion of the skeletogenous layer (and this means, in other words, that it is formed earlier and earlier during the ontogenetic development), prevent the ossification and calcification of this part of the centrum. We know that its cells retain, throughout life, their juvenile quasi-embryonic character. It is, however, neither centrum nor arches, but only a non-segmented neural tube, which is produced by this process of regeneration. The reproduction of centra is precluded by the previous normal reduction of or suppression of the chorda, around which alone they could be formed, unless we establish a far-fetched analogy with the epichordal type of certain Anura.*

The divided caudal vertebræ bear a great resemblance to those of certain Permian fossils, e.g., Diplovertebron; our ignorance of their detailed structure makes any discussion of them unprofitable.

Lacerta vivipara; ripe embryos. (Figs. 24–32.)

The chorda is still present throughout the trunk and neck ; its sheath is reduced to the Elastica externa. The disappearance of the E. interna lets the E. externa come to lie very near the chordal epithelium, but it also explains why these two often make common cause and shrink away from the skeletogenous layer.

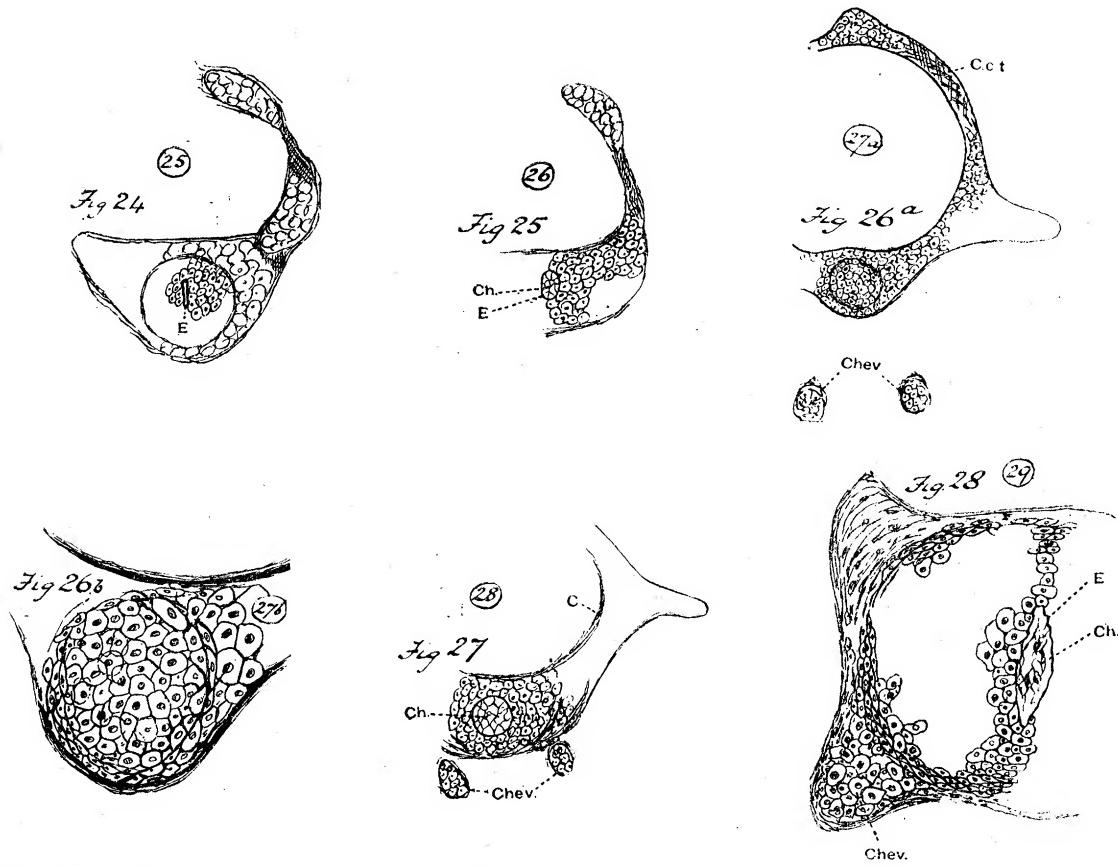
The axial column consists, in this stage (fig. 30), of a continuous tube of more or less ossified cartilage, without any intervertebral joints, resembling, in this respect, that of the Geckos.

In the neck, trunk, and tail the neural arches rest, with their broad bases, upon the central portion, the neighbouring arches nearly touching each other. Anterior and posterior zygapophyses are already imbricating.

* Artificially mutilated tails, by scalpel or scissors, do not regenerate so certainly as those which are allowed to break off, because there is a great probability that the knife makes an unnatural division, either too far in front or behind the septum : lastly, if the septum itself is hit, many of its cells will be injured and the experiment is then likewise doomed to failure.

The spinal nerves issue between the arches, in level of the future joints ; the dorsal roots slightly more cranialwards than the ventral roots.

Unpaired basi-ventral cartilages are present in the first five cervical vertebrae (fig. 30). The first is very large, and forms the ventral semi-ring of the atlas ; the second is beginning to fuse with the future second centrum ; the third is hook-shaped. These basiventral elements lie in the same transverse level with the neural arches ; the sixth vertebra possesses only a thickening of connective tissue in the outer layer



Figs. 24 to 28. Transverse sections through the tail of a ripe embryo of *Lacerta vivipara*, a reconstruction of which is shown in fig. 29. The encircled numbers refer to the levels of these sections, as indicated by the small numbers in the axis of the chorda of fig. 29. Fig. 26b represents the axial portion of the section of 26a as seen under stronger magnifying power. For further explanation see text, p. 35.

of the membrana reuniens. In the thoracic, lumbar, and sacral regions, these ventral elements are absent. They reappear on the fourth caudal as paired chevrons, they lie, however, no longer in the same level with the neural arches, but have moved headwards into an intervertebral position.

The chorda is of very variable thickness, showing widenings or swellings, and constrictions, which are, of course, correlated with the thickness of the surrounding tube of cartilage.

In the neck, in median sagittal sections, the chorda is widest in the intervertebral regions, for instance, in Sections 93, 135, 170 of fig. 30, and the skeletogenous layer is comparatively thin. Intravertebrally, in level of the neural arches, the chorda is much restricted owing to the growth of large cartilaginous cells. It is, however, only in sagittal sections that the chorda assumes the regular hour-glass shape. Transverse sections show the chorda to assume various shapes according to the side whence the growth of surrounding cartilage is most rapid. The chorda is, for instance, reduced to a thin rod, and retains its position in the longitudinal axis in Sections 77 to 80 ; it is likewise round and small, but with more cartilage below it in Sections 103 to 109 ; in Sections 144 and 183 the new cartilage lies entirely below the chorda, which is, therefore, driven into a dorsal position.

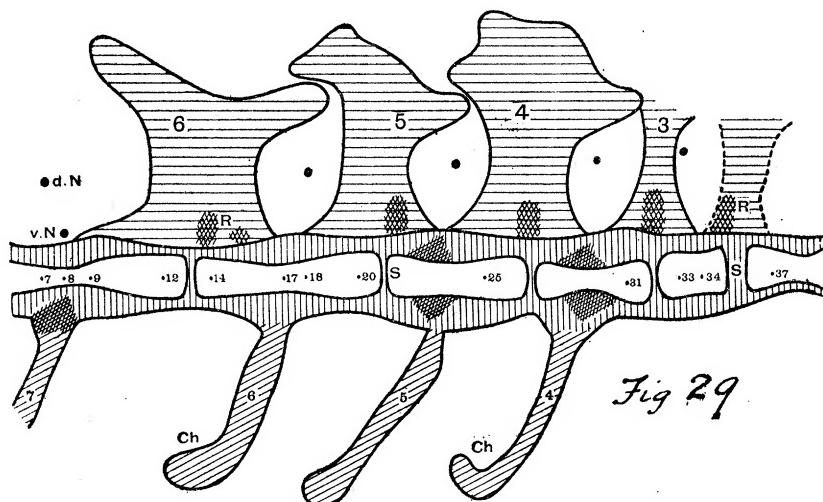


Fig. 29. *Lacerta vivipara*, ripe embryo. Diagrammatic reconstruction of a portion of the tail. The neural arches and the chevrons lie of course more lateral to the vertical longitudinal section in which the central portion of the column is represented.

The chorda is left white, interrupted by cartilaginous septa in the middle (intravertebral) of the 2nd and 6th postsacral or caudal vertebrae. The first chevron belongs to the fourth caudal vertebra.

The small numbers in the central line of the chorda refer to the sections described in the text.

The attachment of the ribs is indicated by strong cross-lines. Dense cartilage, indicative of intervertebral joints, is slightly cross-shaded.

d.N. = position of origin of the dorsal roots of spinal nerves.

The actual length of the portion figured, from 7 to 37, measures 3 millimetres.

In other regions the chorda is reduced to a narrow vertical slit ; for instance, in sections 33, 38 (see also figs. 24 and 28), where the cartilage is equally thick above and below ; also in sections 30, 31, 61, 63, 69, where the cartilage is thicker below than above, thickest, of course, laterally.

The intravertebral constriction is carried to the extreme in the tail (fig. 29), because there, in level of the middle of the neural arches, the cartilage forms a transverse

septum, as is the case also in Geckos, but this septum is narrow. In these caudal vertebrae the chorda is, moreover, constricted in level of the spinal nerves, and this second constriction, which is brought about by a thickening of the apparently intervertebral cartilage, coincides with the shifted position of the chevron-bearing basiventral elements. Here the chorda is reduced to a vertical slit.

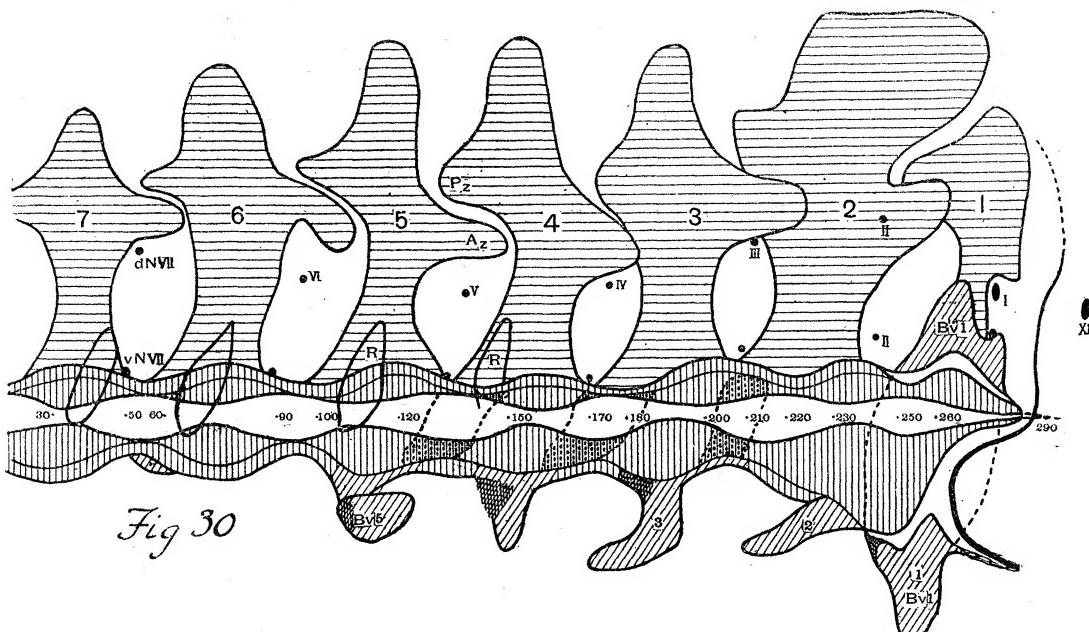


Fig. 30. *Lacerta vivipara*, ripe embryo. Diagrammatic reconstruction of the first seven cervical vertebrae, from a continuous series of about 300 transverse sections. The numbered dots inside the chorda (left white) refer to the ordinal numbers of the sections, some of which are shown in figs. 31 and 32.

1 to 7 = neural arches of the seven vertebrae.

I. to VII. = position of origin of the dorsal and ventral roots of the spinal nerves.

XII. = Hypoglossus.

The basidorsal elements or neural arches are ruled horizontally; the central mantle of the column is ruled vertically; the basiventral elements are ruled obliquely.

The extent of the lateral portion of the first basiventral (ventral half of the atlas-ring) is indicated by dotted lines.

The extent of attachment of the ribs on the fourth to seventh vertebrae is indicated by thick black lines.

The dotted areas within the central mass (for instance, in level of sections 200 to 210), show the extent of the denser cartilage indication of joints.

The cartilage which forms the transverse septa in the tail, and in the trunk and neck, the similarly intravertebral constrictions, is the so-called chordal cartilage, Chorda-Knorpel. It can be asserted with absolute certainty that such a kind of cartilage does not exist, if thereby be understood cartilage which is produced by the conversion of chorda cells. Nor does this cartilage invade the chorda. Consecutive sections allow the Elastica externa to be traced as a continuous, unbroken line, which

becomes irregularly folded, or creased, as the sections approach the septum. The cartilage of the latter is nowhere in direct contact with the cells of the chorda. These two tissues might, however, well be in contact, because it is obvious that the elastica must be broken, or destroyed, somewhere, when the septum is complete, unless the elastica pierces it like a string, but in this case the chorda itself would be reduced to nothing.

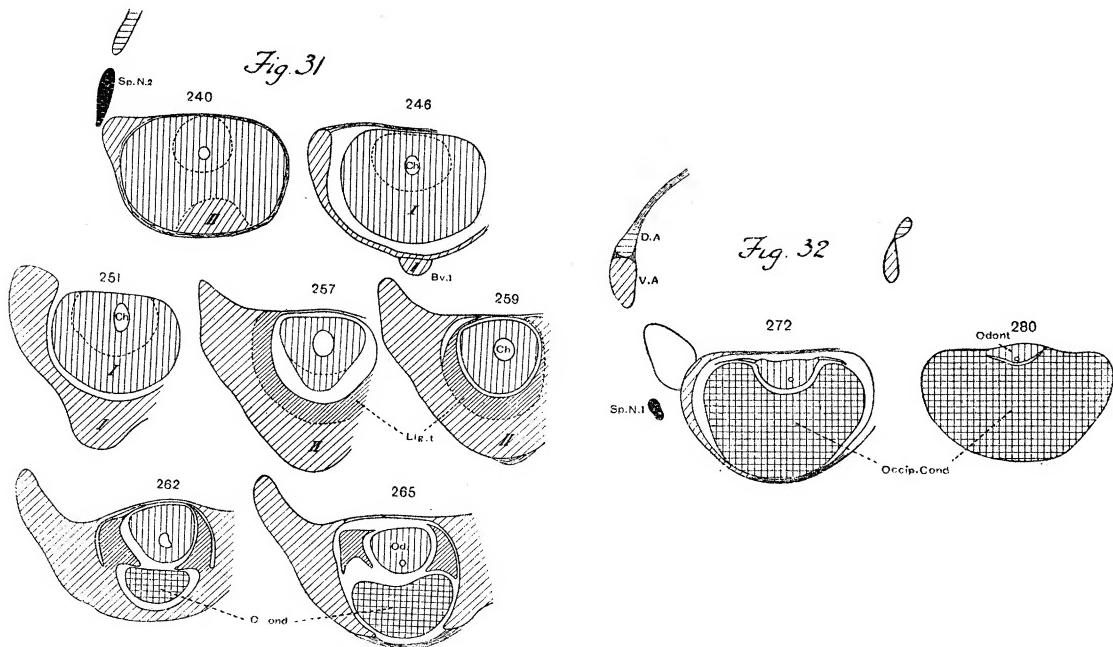
In reality, it is easy enough to understand the formation of this septum by comparing it with the less advanced condition in the cervical vertebrae. Nowhere is the elastica pierced or perforated by cartilaginous cells of the outer surrounding skeletogenous layer. Those authors who figure and describe such an immigration in Amphibia and in Reptiles (especially since we know that such a change does take place in many Fishes) have seen sections like the one figured of Section 27a, or sections which cut through the bases of the chevrons. The same applies to the drawing of the reconstructed tail of the Gecko. The cartilage, namely, which causes the intravertebral constriction, is of comparatively young date. It begins to grow after the rest of the skeletogenous layer has begun to assume its final shape and features, when, moreover, calcification and perichondral ossification has made its appearance. The cells of the inner side of the thickening ring retain for a long time the features of embryonic new cartilage, and therefore look different from the surrounding older cells. The irregular calcification coincides, of course, with the level of the original peripheral extent of the unconstricted chorda, and this system of streaks has been mistaken for the torn or perforated elastica. This mistake has been fostered by the further circumstance that, in the intervertebral region, the cells of the centrum proper become smaller peripherally, flattened or spindle-shaped, producing an appearance as if the centrum were sharply separated from a cortical layer which contains the arches.

Section 29 (tail of *Lacerta*, fig. 28) passes through the middle of the intercentral disc, which gives an impression as if it were marked off against the chevrons as well as against the dorsi-lateral wings, which are the most anterior spurs of the base of the fourth neural arch. These wings are a cortical layer, and do not belong to the disc, but the chevrons are continuous with that disc.

The case is different in those sections which pass either a little in front or behind the intercentral disc, namely, through the neurocentral suture, and through the base of the intercentral wedges, where these latter expand and overlap the centra. This is best seen in the region of the ventral piece of the atlas ring and the odontoid, less obvious in the other cervicals. Here we can speak of a cortical zone, which contains the dorsal and ventral arches, and of an inner core which belongs to the centrum. It is probably this condition which has caused HASSE and others to conclude that centra and arches are originally one mass, that the centra are produced by rapidly-multiplying cells, which from the neighbourhood of the bases of the arches break through the elastica and transform the chordal sheath into centra. Such a building up might

possibly be applicable to an ideal vertebra which combined Reptilian with Urodelous features, provided the bodies of the Urodelous vertebra were composed of the same arcualia as those of the *Amniota*.*

The atlas and the epistropheus require special attention. The accompanying figures of Sections 240 to 280 (figs. 31 and 32) show the gradual diminution of the



Lacerta vivipara. Newborn. Seven transverse sections through the first cervical vertebra.

The numbers enclosed in circles refer to the sectional levels indicated in fig. 30.

The centrum, odontoid process, is ruled vertically; the basiventral elements are ruled obliquely.

centrum and of the chorda. The dotted line, at some distance from the chorda, in Sections 240–257, indicates the original extent of the chorda, all the cartilage within the dotted line being practically so-called chorda-cartilage, while the rest of the centrum is produced by the ordinary thickening of the skeletogenous layer, and is serially homologous with the swellings of cartilage in the tail, headwards and tailwards from the cartilage of the chevron-bearing disks, for instance, in Sections 9 and 18 (fig. 29).

Lacerta vivipara. Newborn. Sections 272 and 280; cf., fig. 30.

Section 272 crosses the first spinal nerve, outside the vertebra.

Section 280 cuts the foremost end of the odontoid process and the most anterior rim of the atlas-ring.

* It has been explained on p. 14 that the bodies of the Urodelous vertebræ are pseudocentra, because they are formed entirely by the combined basidorsal and basiventrals, which grasp round the chorda and co-ossify, the interbasalia forming the intervertebral articular portions. In the *Amniota* the vertebral bodies are true centra, because they are pieces which are composed of the interbasalia, and which, only later on, have come to carry the basidorsalia or neural arches, and, eventually, the remnants of the basiventralia, namely, ribs and intercentra.

Basiventral I. grasps back, tailwards, to the level of Section 240, where its outer coat of connective tissue merges into that of the basal spur of the second neural arch, and it covers the cranial portion of Basiventral II.

In Section 246, Centrum I., and Basiventral I. are separate; in Section 251 the basiventral mass forms a thick semi-ring, the lower half of the atlas ring, with its haemal thickening. Sections 257 and 259 show the gradual formation of the ligamentum transversum atlantis, which would be serially homologous with menisci or intervertebral disks or pads, if such were not suppressed in Lizards.

Section 262 passes through the caudal end of the occipital condyle. Section 272 goes through the cranial extension of the atlas ring. The first spinal nerve arises in level of 275. Section 280 belongs entirely to the occiput, just touching, however, the dorsal and ventral halves of the atlas ring near their junction.

SPHENODON. (Fig. 33.)

This reptile resembles in many respects the Geckos in the primitive structure of its axial skeleton.

Intercentra are present from the atlas to the end of the tail. The first intercentrum is very broad and thick, and forms the ventral half of the atlas ring, which

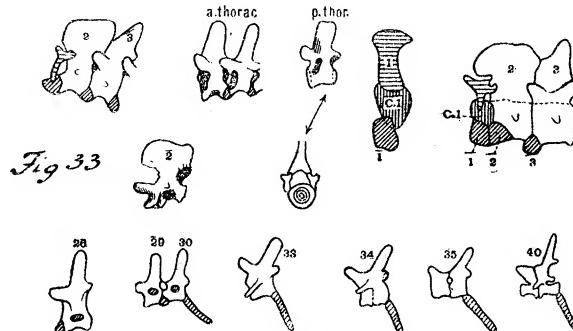


Fig. 33. *Sphenodon punctatum*, adult. Camb. Mus. Left-sided views of vertebræ. The numbers refer to the ordinal numbers of the vertebræ, beginning with 1 = atlas.

The 26th vertebra is the first sacral, with its basiventral elements attached in front; the 30th vertebra, third caudal, carries the first pair of typical chevrons. The 34th shows an indication of the division of the centrum into an anterior and a posterior portion.

The basiventral elements (intercentra, chevrons) are ruled or shaded obliquely; the neural arch of the atlas or first basidorsal element is ruled horizontally; the odontoid or first centrum is ruled vertically. The rib-bearing facets of the thoracic, sacral, and first caudal vertebræ are indicated by shaded areas.

One of the posterior thoracic vertebræ is also represented in an anterior view.

articulates with centrum I. and with intercentrum II.; the irregularly shaped neural arches remain separate from each other and from the basal piece: they carry on the dorsal side a pair of disconnected supradorsals, the so-called pro-atlas.

The second intercentrum is fused with centrum I. and II. The second to 8th or 9th intercentra carry low median ridges or knobs, and are, as a rule, more firmly attached to the cranial ends of the centra. From the 3rd or 4th caudal vertebra backwards, they appear in the shape of chevrons, and articulate more with the vertebra in front than with the one which follows behind. The bases of the right and left chevrons are frequently fused across, so that the caudal canal is completely surrounded by bone.

Every intercentrum, be it a pair of chevrons, or an unpaired nodule, or crescent, extends dorsalwards into a fibro-cartilaginous ring which surrounds the chorda. The centra of the vertebræ are deeply amphicoelous; the cavity is filled, throughout life, by the chorda. The rest of the centrum is solid.

Most of the caudal vertebræ are transversely divided into two parts, the posterior of which carries the greater share of the arches.

The first three ribs are represented by bands or ligaments of connective tissue without cartilage or bone. The first is attached to the side of the first intercentrum; the second arises from the second intercentrum and forms a small tubercle on the side of the second centrum; the third behaves similarly. The vertebral arteries and the lateral strands of the sympathetic chain pass through these double basal attachments of the reduced ribs. The other ribs are osseous; they possess short capitula which retain their partly intercentral attachment, while the tubercula are carried by low processes of the centra. Already in the thoracic region both capitulum and tuberculum merge into one facet, at first dumb-bell shaped, further back oval, which is gradually conveyed further tailwards, upon the middle of the centrum, and also dorsalwards, until the facet reaches, and ultimately covers, the neuro-central suture.

The first few caudal vertebræ also possess ribs, which are, however, very short, and fuse with the diapophyses, immediately below which lies the neuro-central suture.

CROCODILIA. (Figs. 34-38.)

Remnants of the chorda persist in the middle of the centra. These are, in recent crocodiles, mostly procoelous, but the first caudal is strongly bi-convex.

Cartilaginous intercentral rings, pads, or menisci, occur regularly throughout the vertebral column, unless they are abolished by fusion of adjoining vertebræ. It is most instructive to follow the attachment of the ribs in one and the same individual. The position of the capitulum, vertically below the tuberculum in the neck, changes in the thorax into one in which the capitulum lies headwards from, and in the same horizontal plane with the tuberculum.

Some of the anterior caudal vertebræ (fig. 37) carry short ribs, which are attached upon the neurocentral suture; long before maturity they fuse with their vertebræ and then look like transverse processes. CLAUS (Lit., No. 24) was the first who showed the existence of such caudal ribs in crocodiles and tortoises, and, as the same

vertebræ carry chevrons besides, he naturally concluded that ribs and chevrons are not the same elements.

The atlas and the epistropheus are of supreme interest (figs. 34 and 37). Crocodiles are, in fact, the only animals in which these vertebrae retain all their constituent hard parts in an almost undisturbed primitive condition.

The basal piece of the atlas, the first basiventral or intercentrum, carries a long rib, which is movably attached by its capitulum. This rib still retains in many specimens a small knob or excrescence on its dorsal edge, which is the last remnant of the tubercular portion. This tuberculum was still complete in mesozoic crocodiles, for instance, in *Metriorhynchus*, in which it articulated upon a prominence which was formed conjointly by the first and second centra.

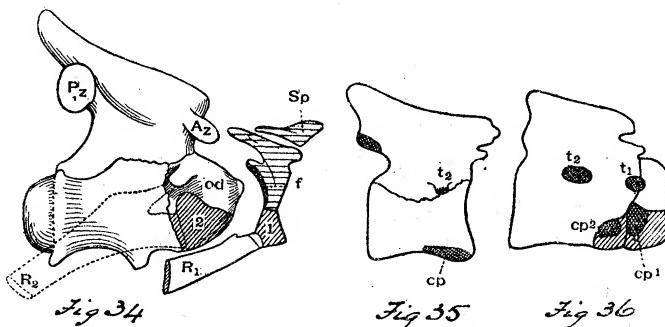


Fig. 34. *Crocodilus vulgaris*. Adult. Camb. Mus. First and Second cervical vertebrae. The second rib is dotted in outline. *f.* = articulating facet of the neural arch of the atlas, playing upon the odontoid process.

Fig. 35. *Steneosaurus*, sp. Jurassic. England. Brit. Mus. Specimen described by HULKE. Second cervical vertebra, showing the neurocentral suture, the capitular and tubercular articulating facets of the second rib.

Fig. 36. *Metriorhynchus*, sp. Jurassic. England. Brit. Mus. Specimen described by HULKE. Atlanto-epistropheal complex. The articular facets of the first and second rib are carried by the first and second right basiventrals respectively. The first tubercular facet is slightly shifted backwards, and lies across the suture between the first and second vertebrae.

The first centrum joins that of the second vertebra, not directly, however, but by the intercalation of the complete second basiventral, namely, by a cartilaginous disk (seriously homologous with the ligamentum transversum of the atlas), and by a large unpaired pyramidal piece (seriously homologous with the ventral half of the atlas ring). This basiventral intercentrum is wedged in from below between the odontoid and the second centrum.

This second basiventral, which soon fuses completely with the first and second centrum, has hitherto been overlooked. It is of all the greater importance because it is this piece (not the odontoid, as has been universally stated and figured) which carries the capitulum of the second rib, the tuberculum of which articulated in *Metriorhynchus* and *Steneosaurus* upon a facet of the second neural arch, or also upon the second

centrum. In recent Crocodiles this tuberculum is slender, reduced, and, curiously enough, is attached to a knob which belongs to the odontoid. This explains the apparent anomalous condition that "the atlas carries two pairs of ribs, the second vertebra none."

The second vertebra of *Steneosaurus* (fig. 35) is not a compound epistropheus; the first centrum is not fused with it; but, to judge from the large articular surface on

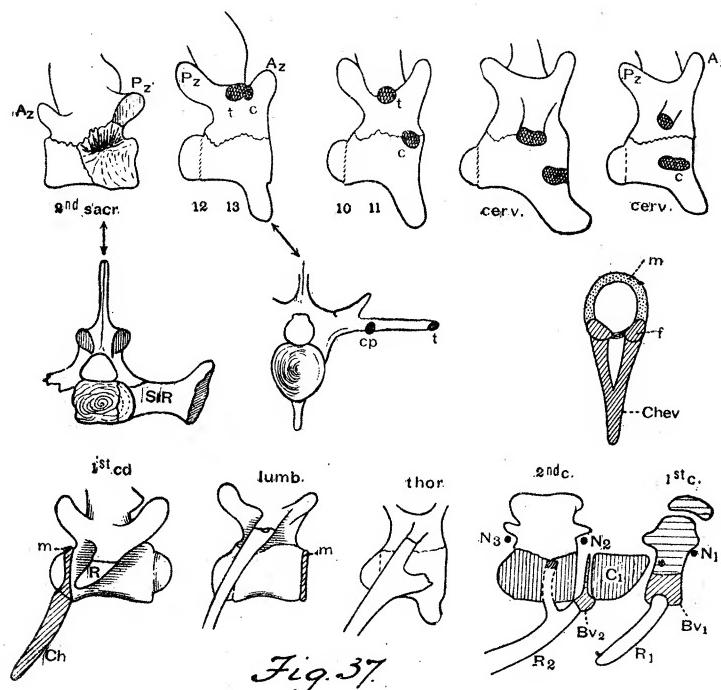


Fig. 37. *Crocodylus acutus*, young specimen, about 5 ft. in length.

2nd sacral vertebra seen from the left side after removal of the sacral rib, the broad attachment of which is indicated.

The same vertebra seen from behind, with the sacral rib, *S.R.*, attached; observe the extent of the central articular facet, which is formed by the centrum proper and by part of the rib.

The 12th and 13th, 10th and 11th, a posterior and a middle cervical vertebra show the changing positions of the capitular (*c.*) and tubercular (*t.*) attachments.

The right figure in the middle series shows a front view of a pair of chevrons; *f* = facets articulating with the posterior end of the centrum of the next previous vertebra. *m* = cartilaginous meniscal ring.

The lower series shows the first caudal, a lumbar and thoracic vertebra, and the analysis of the first and second cervical vertebrae. (Cf. fig. 34.)

the ventrolateral cranial corner of the second vertebra, the basiventral seems to be firmly fused with the cranial end of the second centrum, at least in the specimen which has been described and figured by HULKE (Lit., No. 64), and which is now in the Museum of Natural History, London.

To judge from specimens of *Metriorhynchus* (fig. 36) in the same collection, the

reverse seems to have taken place, namely synostosis between the first and second vertebrae.

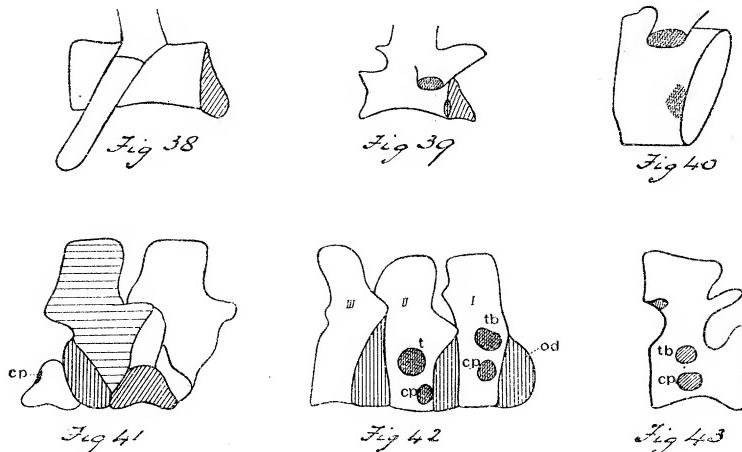


Fig. 38. *Metriorhynchus* sp. Jurassic, Europe. Brit. Mus. Trunk vertebra.

Fig. 39. *Embolophorus dollooverianus*, COPE. Permian, Texas. Brit. Mus. Trunk vertebra. The capitular facet extends across the suture between the centrum and the intercentrum.

Fig. 40. *Pareiasaurus bombidens*, OWEN. Permian, S. Africa. Brit. Mus. Cervical vertebra minus the intercentrum.

Fig. 41. *Eryops megacephalus*, COPE. Permian, Texas. Brit. Mus. Two trunk vertebrae.

Fig. 42. *Cricotus hypanticus*, COPE. Permian, Texas. The first three cervical vertebrae, according to COPE.

Fig. 43. *Nothosaurus mirabilis*, Münster. Trias, Europe. Brit. Mus. Cervical vertebra.

CHELOMIA. (Figs. 44-50.)

The accompanying figures show some of the more important features.

The vertebrae are, sometimes in the various regions of the same column, opistho-, pro-, amphicelous, or even biconvex. The chorda remains longest within the middle of the centrum. Intercentra occur regularly on the first two or three cervicals, in the tail as paired or unpaired nodules, or as short chevrons, which articulate mostly with the caudal ends of the centra, and occasionally fuse with them. Intercentral, fibrocartilaginous disks occur likewise regularly, mostly in the shape of rings; the first is the ligamentum transversum.

The ribs develop originally in the same transverse level with these disks, and frequently the thoracic ribs retain this intercentral position throughout life. The drawing of *Chelone midas* shows the gradual change from the intercentral to a more central, and ultimately to a neural arch attachment.

The neural arches of the thoracic region are likewise intercentral in position. In young tortoises, for instance, the neural arches, the intercentral disks and the ribs are continuous, and lie in the same transverse level, in front of their centrum. They behave, therefore, in exactly the same way as the ring of the atlas with regard to the first column, for instance, in *Trionyx hurum*. Later on the bases of the neural arches

extend head- and tailwards; they, and the ribs, ossify, while the axial portion of what corresponds exactly with the "primitive Wirbelbogen" of FRORIEP (see Aves and Mammalia) is reduced to a peripheral annulus fibrosus.

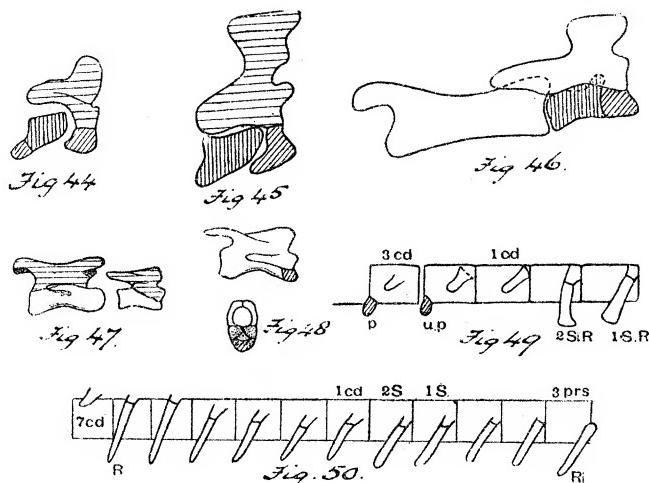


Fig. 44. *Trionyx hurum*. Adult. Cambridge Mus. Atlas; the second intercentrum is attached to the posterior end of the centrum.

Fig. 45. *Trionyx gangeticus*. R. Coll. Surg., London. Adult. Atlas.

Fig. 46. *Chitra indica*. R. Coll. Surg., London. Adult. The first and second cervical vertebræ.

Fig. 47. *Platemys*, sp. Adult. The first and second cervical vertebræ.

Fig. 48. *Chelys matamata*. Cambridge Mus. Half-grown. Atlas from the right side; below as seen from in front.

Fig. 49. *Macroclemmys Temmincki*. Cambridge Mus. Diagrammatic representation of the position of the first and second sacral rib and those of the three first caudal vertebræ. The second caudal carries an unpaired, the third a paired "intercentral" or basiventral element.

Fig. 50. *Chelone midas*. Cambridge Mus. Diagrammatic representation of the position, length and attachment of the ribs with reference to the third presacral to the seventh caudal vertebræ.

In *Trionyx hurum*, *T. gangeticus*, *Chitra indica*, *Clemmys sigris*, *Testudo*, and in many others, the various pieces of the atlas do not ankylose, and the first centrum remains also movably attached to the second, although it sometimes carries and fuses with the second intercentral piece. In *Platemys* and in *Chelys matamata* all the constituent parts of the atlas co-ossify, and form a complete, solid vertebra, which articulates by a concave-convex joint with the centrum of the second vertebra. The normal number of cervical vertebræ is 8 in all Chelonians.

The first spinal nerve issues between occiput and atlas, all the others behind the neural arches of their vertebræ.

AVES. (Figs. 51-55.)

FRORIEP (Lit., No. 46) has published an excellent account of the development of the cervical vertebræ of the chick. His results are as follows:—

End of the 4th day.—The thin chordal sheath is surrounded by the skeletogenous layer (FRORIEP's perichordales Bindegewebe), which is thicker ventrally; it envelops the spinal nerve roots and ganglia, and extends outwards into the intermuscular septa. These metamerous masses of the skeletogenous layer he calls the "primitive Wirbelbogen."

Middle of the 5th day.—The "primitive Wirbelbogen" consists of a perichordal ring, which extends dorsally in the shape of dorsal arches, while ventrally the ring is thickened into a hypochordal clasp (Spange). The perichordal ring consists of bundles of longitudinal fibres, while the arches and the clasp consist of "chondrogenous" tissue, *i.e.*, "Vorknorpel," or prochondral tissue of other authors.

End of the 5th day.—The perichordal ring is now thickened, consists of fibrous tissue, and forms the rudiment (Anlage) of the future intervertebral ligament. The right and left dorsal arches extend upwards and slightly tailwards from this ring; ventrally they are connected by indifferent tissue with the hypochordal clasp, which has become cartilaginous, and has assumed the shape of a horseshoe, with the free arms looking upwards. The presence of a right and left vertebral artery (produced by lateral communicating branches of the interprotovertebral arteries) makes it possible to distinguish in each arm of the hypochordal clasp a neural arch and a rib, or, at least, the levels or points to which the capitula and tubercula of the future ribs will be attached. A new thickening cluster has appeared in the skeletogenous layer, slightly behind the hypochordal clasp. This new cluster is unpaired, it is thickest laterally and ventrally; during its growth it grasps round the chorda from below upwards, behaving, in fact, like a second posterior horseshoe.

Middle of the 6th day.—The unpaired ventral cluster has transformed itself into a cartilaginous ring, which surrounds the chorda almost completely, being the foundation or beginning of the centre or body of the vertebra.

Headwards this centre touches the hypochordal cartilage, the arms of which are now in connection with the likewise cartilaginous dorsal arches. The latter are, however, still open above the spinal cord.

Fusion of the central cartilage with the anterior mass, which contains the neural arches, the hypochordal clasp, and the intervertebral ring, produces the complete vertebra. The latero-ventral corners of the clasp show a thickening of their perichondrium, which extends laterally into the intermuscular septa as dense fibrous tissue, and indicates the future ribs.

The spinal nerve issues originally immediately behind the neural arches, but later on the nerve comes to lie in level of the posterior portion of the centrum and in front of the hypochordal cartilage of the vertebra next behind. This apparent shifting of the position of the nerve is caused by changes of the relative growth of the skeletal parts. The centrum grows chiefly headwards in length, and comes to lie with its somewhat conical apex between the arches, in the same way as the odontoid process, the centrum of the atlas, is grasped by the arches of the atlas.

Towards the close of the sixth day the cartilage of the centra has surrounded the chorda completely; the latter lies, however, still nearer the dorsal side.

The hypochordal masses of cartilage are gradually reduced and disappear, with the exception of the first and second, and those of some of the caudal vertebræ.

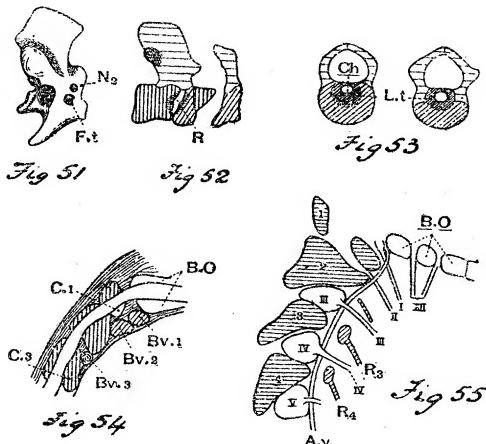


Fig. 51. *Bucorvus abyssinicus*. Adult. Camb. Mus. The first and second cervical vertebræ fused into one physiological unit.

Fig. 52. Diagram of the first and second cervical vertebræ of a young Bird.

Fig. 53. The atlas-ring of a young Bird; front (right) and back view (left).

Fig. 54. The first three cervical vertebræ of a Chick, ninth day of incubation.

Sagittal section. After FRORIEP.

B.O. = Basioccipital.

I., II., III. = Centra, perforated by the chorda dorsalis.

Bv., 1, 2, 3 = Basiventralia; FRORIEP's hypochordal elements.

Fig. 55. Vertical longitudinal section, in a plane lateral to the centra of a Chick-embryo of the ninth day. After FRORIEP.

XII. = N. hypoglossus.

R., 3, 4 = Third and fourth rib.

Sp.G., 5 = Ganglion of the fifth spinal nerve.

FRORIEP did not discuss the morphological homology of these hypochordal cartilages, but he hinted at their probable homology with the "Haemal-Bogen," or caudal chevrons of Reptiles. Moreover, he pointed out that the two first vertebræ retain more primitive features, because their several constituent parts remain more or less separate. Indeed, he deserves the credit of having explained their composition. The first hypochordal (which is equivalent with the first pair of basiventralia) grows to a considerable size, and forms with the neural arch (first pair of basidorsalia) the ring of the atlas. The first centrum (equivalent with the first pair of interventralia) joins the second vertebra as its odontoid process, but it does not fuse directly with the second centrum, there being interposed between the first and second centrum the whole of the second hypochordal mass, which originally forms an intervertebral, or intercentral pad, between the first and second centrum. The atlas-ring (fig. 53), or

rather its so-called "lower, unpaired half," *i.e.*, the first pair of basiventralia fused into one mass, articulates solely with the cranial surface of the second hypochondral mass, but not with Centrum II. The neural arch of the second vertebra is shifted backwards upon the Centrum II., forming with it the first neuro-central suture. The innermost portions of the ventral half of the atlas-ring do not ossify, but remain cartilaginous or fibrous, and form in the adult Bird the ligamentum transversum atlantis. It grasps round the odontoid process, and is perforated by the remnant of the chorda. This ligamentum transversum is serially homologous with the "intervertebral pad" between the odontoid and the centrum of the epistropheus. It is also homologous with the intervertebral pads which exist between any successive vertebræ, in the shape of the so-called menisci or annuli fibrosi. These have been well described by JAEGER (Lit., No. 67), who in his carefully-written paper had already drawn attention to the important fact that the atlas-ring does not articulate with the Centrum II., but with a separate element interposed between the first two centra. He had also shown the ligamentum transversum and the menisci to be serially homologous structures. The centre of each meniscus is, of course, perforated by the chorda dorsalis, the last trace of which remains as the ligamentum suspensorium corporum vertebralium; the first or foremost of these is the better known ligamentum suspensorium dentis epistrophei.

Originally, and FRORIEP has been able to show this in the younger embryonic stages, the ribs are carried entirely by the basiventralia, but they are soon transferred upon the centra, which produce lateriventral processes which carry the capitulum, and upon the dorsilateral processes or outgrowths of the neural arches, which carry the tubercular end of the rib. In all birds each rib is carried by the centrum and by the neural arch of the vertebra to which it belongs. Intervertebral articulation of the capitulum does not occur.

The first spinal or sub-occipital nerve passes in front of the atlas, sheltered thereby often in a little notch at the cranial margin of the neural arch of the atlas; sometimes this notch is transformed into a foramen owing to subsequent osseous growth.

The second, and the following spinal nerves, issue immediately behind the neural arches of their vertebræ; they appear now in an intervertebral position owing to the great caudal extension of the neural arches over their centra, but the roots of the nerves arise considerably further headwards, indicating thereby their original intra-vertebral nature.

The Bucerotidæ, Buceros, as well as Bucorvus, are noteworthy, because they are apparently the only birds in which the whole of the first and second cervical vertebræ completely co-ossify into one physiological unit (see fig. 51).

Many birds possess on the ventral surface of many vertebræ median bony out-growths in the shape of vertical longitudinal blades, or in L shape, which serve for the more advantageous attachment of the long flexor muscles of the neck, and are on no account to be confounded with hæmal arches or other basiventral elements.

MAMMALIA. (Fig. 56.)

FRORIEP's second paper (Lit., No. 47) deals with the embryonic development of the cervical vertebrae of mammals, especially *Bos*. Many of the salient features have been corroborated by MACALISTER (Lit., Nos. 71, 72) in human embryos.

In the cow embryo of 8·7 millims. length of body the separation of the sklerotomes from the myotomes is still incomplete. There is not yet any cartilage, but the spinal nerves lie behind the "primitive Bogen." The space of the future bodies of the vertebrae is still occupied by embryonic connective tissue.

In the embryo of 8·8 millims. the thickness of the chorda amounts to 0·03 to 0·05 millim., the constrictions coinciding with the cranial ends of the primitive arches. The chordal sheath is only $2\mu = 0\cdot002$ millim. in thickness.

In embryos of 12·0 millims. the chordal sheath has become still thinner, measuring from 0·06 to 0·025 millim. The primitive arch is differentiated into a neural arch, an intervertebral disk, and a hypochordal mass, the first and the last being already partly cartilaginous. Tailwards from and below the chorda has appeared a mass of hyaline cartilage, the beginning of the future centrum; this mass is bilaterally symmetrical, with indications of being composed of a right and a left piece.

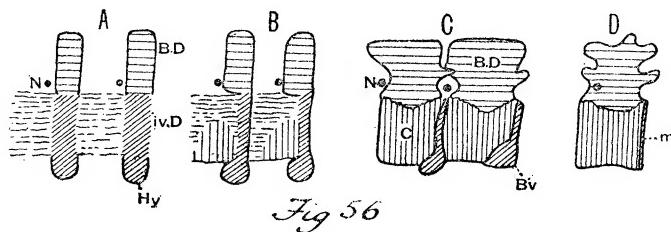


Fig. 56. Diagrammatic representation of four stages in the ontogeny of two mammalian trunk-vertebrae.

Stage I. of the "primitive arches,"
each of which is composed of

Neural arches = Basidorsalia. Invertebral disk = axial portion of Hypochordal mass = ventral portion of	} Basiventralia.
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In embryos of 18·5 millims., which correspond with human embryos of two months, the chorda itself has mostly shrivelled up, while the chordal sheath has become partly invisible, especially in region of the centra. The diameter of the chorda is 0·055 millim. within the centra, 0·025 millim. in level of the disks, i.e., in level of the primitive arches. The vertebral arteries are completed. The neural arch is quite cartilaginous. The hypochordal elements are cartilaginous only below the chorda, but they grasp already upwards into the disk, which connects them with the neural arches. Such hypochordal cartilages occur between all the vertebrae. The cartilage of the future centre has grown into a ventral horse-shoe or semi-ring, which more or less grasps round the chorda.

In embryos of 22·5 millims. ossificatory centres have appeared, one pair in the neural arch, another pair, which soon fuses into one, in the centrum. The neural arches

have moved on to the centrum, which is now completed; the spinal ganglia are shifted into the level of the intervertebral disk,* the roots of the nerves arising however still immediately behind, or even within the region of the neural arch.

The hypochordal cartilages are reduced and disappear, only the first and second remaining.

In embryos of 26 millims. only the first hypochordal remains cartilaginous. The second persists as dense connective tissue, having lost its cartilage, and having severed its connexion with what henceforth can be called the second intervertebral disk.

Ultimately the chorda disappears within the centra, but it remains in the middle of the disk, where it originally was pinched in. Considering that this is the place of the nucleus pulposus of the adult vertebral column, it follows either that this portion of the chorda enjoys long continued growth, although to a meagre extent, or that neighbouring parts of the disk itself, together with the chorda and its sheath, undergo some pulpy degeneration.

The final composition of the Mammalian vertebrae is as follows:—

The atlas ring is formed, as usual, by the first pair of basidorsalia (neural arch) and by the first pair of basiventralia (first hypochordal cartilage or bone ligamentum transversum). The first centrum joins that of the second vertebra, but owing to the complete suppression of the second hypochordal element, the caudal portion of the first centrum broadens out considerably, spreading over the whole cranial surface of the second centrum. Consequently, as FRORIEP has pointed out, the ring of the atlas articulates with the first centrum, but not, as in Birds (and Reptiles), with the second hypochordal and its disk. To emphasize this important feature, apparently peculiar of the Mammalia, we can with advantage express it as follows:—The first trochoid joint, namely, that between the atlas and the epistropheus, is an intervertebral joint in Reptiles and Birds, but an intravertebral joint in Mammalia. The following joints of the Mammalia are all intervertebral, because they pass between the caudal surface of the centrum of the anterior vertebra and the cranial surface of the body of the vertebra next behind, the meniscus or intervertebral pad belonging genetically to the cranial end of its own vertebra.

In the majority of Mammals the ring of the atlas co-ossifies into one solid unit, its ventral half being composed of the first basiventral mass. But in some Marsupials, *e.g.*, *Thylacinus*, this “unpaired ventral piece” remains as a very small and separate piece of bone, which does not fuse with the neural arch. The reduction of this piece is carried out to the extreme in *Phascolomys*, *Phalangista*, *Macropus*, and others; the right and left halves of the neural arch extend ventralwards, meeting and ultimately fusing below the odontoid with each other. This is an example of the

* It should be remembered that only owing to, and after, the shifting of the neural arches backwards upon their centra, and owing to the reduction of the hypochordal cartilage, the tissue in question becomes an intervertebral ring.

reduction of a whole vertebra, namely, of the atlas, to a neural arch and its centrum. Moreover, it follows that the trochoid joint between this atlas ring and the first centrum is, morphologically speaking, a neuro-central joint.

The basiventralia of the second vertebra do not always disappear, but develop sometimes into a pair of ossicles between the rudimentary rib and the second centrum, behind the ventri-lateral corners of the first centrum. Such a pair has been described and figured by MACALISTER (Lit., No. 72, fig. 8) as hypochordal epiphyses, in the epistropheus of a child of 28 months. In another specimen, of 5 months, one such survival is figured.

In the other cervical and thoracico-lumbar vertebræ of Mammalia, such "inter-central" ossifications are rare, but they occur sporadically as median unpaired nodules of irregular shape. They are, of course, not to be confounded with the central epiphyses of the vertebræ.

Osseous basiventrals, or intercentra, re-occur in the caudal region of many Mammals, for instance, in Cetacea, Edentata, Marsupialia. These bones, carelessly called chevrons, hæmal arches, hæmapophyses, untere Bogen, are usually loosely attached to the intervertebral region. Sometimes they fuse on to the posterior end of the body of the vertebra next in front; the right and left bones remain separate, or they fuse distally, diverging again occasionally.

The *Ribs*, genetically the distal lateral extensions of the basiventralia, still make their first embryonic appearance in the same transverse level with the primitive arch, namely, above the hypochordal elements of FRORIEP. The basis, the original proximal end, is, of course, the capitulum. Owing to the transformation of the axial or ventral portion of the basiventral mass into the intervertebral disk, the rib loses, so to say, its progenitor, and its capitulum comes to lie in the intervertebral space. This more primitive condition prevails in the thoracic ribs of most Mammalia, notably in Monotremes. In them the thoracic and lumbar ribs possess no tubercular attachment. Frequently, however, the capitulum transfers its attachment backwards upon the side of the centrum, a secondary change which applies most commonly to the last two or three ribs. The shoulder, or the tuberculum of the rib, is always attached to a dorso-lateral process of the neural arch of its own vertebra.

The spinal nerves issue behind the neural arches of the vertebra to which they belong. These nerve holes retain their most primitive position in the thoracic and lumbar region of the Monotremes, the foramina lying almost in the middle of the vertebræ. In many cases the foramen is closed posteriorly, caudalwards, by a thin bridge of bone only, which bridge itself is, however, a secondary modification. When the bridge is wanting the nerve passes of course through a notch at the caudal rim of the neural arch; but there are many instances in which normally the exit of the nerve has been so much shifted, owing to special modifications of the neighbouring parts, that the notch is formed in the cranial surface of the arch of the next following vertebra, to which the nerve does not belong. Lastly, an instance of the frequent

enclosure of a spinal nerve by a vertebra, which is not its own, is given by the atlas-ring and the first spinal or sub-occipital nerve. The human anatomist is quite right when he describes eight cervical nerves but only seven vertebræ.

SUMMARY CONCERNING THE AMNIOTA.

Every typical vertebra is originally composed of three principal pairs of elements, namely : (1) *Basidorsalia*, which form the neural arch ; (2) *Basiventralia*, in the shape of a semi-ring, or a complete disk which meets by suture the bases of the neural arches, and which carries the ribs as lateral apophyses, haemopophyses in the tail ; (3) a *centrum*. This centrum lies behind the other pieces, is originally composed of a right and a left portion, which begin to be formed below the chorda, in the ventral half of the skeletogenous layer ; later on the united ventral mass assumes crescent-shape, and ultimately surrounds and restricts the chorda.

In the undisturbed condition (as it is preserved in the atlas) this centrum and the basiventral mass form a square block, or rather a cylinder, which is the whole "body." In conformity with the development of this compound block, the anterior mass is broadest below, pointing upwards, while the posterior mass starts likewise from below but becomes broadest above, reversing its proportions. The proof that the vertebral centra of the Amniota are a compound of, and are equivalent to a pair of ventral arcualia, are the following : Ontogenetic indications, namely their first appearance as ventral thickenings in the skeletogenous layer, the growth into ventral crescents and the ossification from paired centra ; the study of fossils, which alone represent the true phylogenetic record, *cf.* "Comparison of Anura with certain palaeozoic and mesozoic Amphibia and Reptilia," p. 20.

The basiventralia exhibit every stage from complete development to absolute reduction. The axial portion forms either a large ossifying piece, for instance in the atlas of recent Amniota, and in the trunk of many mesozoic Reptiles, *e.g.*, *Metriorynchus*, *Embolophorus*, or it is reduced to the fibro-cartilaginous intervertebral disk or meniscus. The most ventral portions of this disk appear, when ossified, as crescents or nodules, or chevrons, collectively called wedge-bones or intercentra.

The *Ribs* are the offspring of basiventralia, frequently retain their capitular attachment to the latter, more clearly and more frequently in mesozoic than in recent animals. When the axial portion of their basiventralia is reduced, the ribs come to lie either in an "intervertebral" position, or they shift their capitular attachment tailwards, first upon the centrum, then perhaps higher up on to the neural arch. The tuberculum and its attachment to the neural arch is a secondary acquisition made by Amphibia, taken over from them by the Amniota. Tertiary changes, by subsequent reduction of previous acquisitions, affect the ribs in many ways. The rib may lose the capitulum, and, being restricted to the tubercular portion and the old shaft, of course affords a parallel case to what has taken place in Anura. Or the rib may

lose its newly-gained tuberculum and be reduced to its original, now pseudo-primitive, condition with basiventral attachment, *e.g.*, Monotremes.

The chevrons are not ribs, although they are like them produced by the basiventralia, but with this difference, that the ribs are lateral, pleural outgrowths, which form joints with their bases or homes, while the chevrons are more median, or more ventral, outgrowths, which do not sever their connection, or form joints with, their bases. When, however, these very bases are reduced, either to intercentral fibrous discs, or even further, then, of course, their ventral offspring (namely the hæmapophyses, or, in this particular case, the chevrons), will appear in the guise of separate pieces.

This is not an equivocal distinction without a difference. Osseous chevrons, movably attached to osseous discs, are unknown; osseous chevrons, however, attached to fibrous discs or wings are common, but this condition has been brought about by a change, which has a parallel among ribs, namely by the reduction of the axial portion of the basiventral mass. It is conceivable that the hæmapophyses may come to act as carriers of the ribs, but this is a feature which is restricted to Fishes, and does not occur in Tetrapoda.

Anyhow the ribs of all vertebrata are homologous structures. There is no genetic difference between "Amphibian or dorsal," "Amniotic or double," "ventral or Fish-ribs." The ribs and the chevrons, or the sub-caudal paired outgrowths, are both "untere Bogen, lower, inferior arches," if thereby we understand distal portions of the basiventralia. They have to be distinguished by terms. For the one the vernacular, "costæ, côtes, ribs, Rippen," are sufficient, otherwise "pleurapophyses" could be used with advantage, in spite of the original meaning of this term being more than doubtful (OWEN, Archetype). The more median outgrowths, which tend to enclose the sub-caudal vessels, do not always appear in the shape of chevrons, namely, as movable paired pieces; as true counterparts of neural arches or *neurapophyses*, they should be called *hæmapophyses*, hæmal arches, while *hypapophyses* should be restricted to the secondary, paired, or median outgrowths from the ventral surface of the vertebral bodies.

By using OWEN's nomenclature in this sense, the "apophyses" compounded with nouns (neuron, hæma, pleuron) indicate arch-like outgrowths, which tend to surround, enclose, protect; while "apophyses" combined with prepositions (dia, para, hypo) indicate attachments.

SUMMARY OF RESULTS.

The key to the solution of the composition of the vertebral column is given by the metamic repetition of the four pairs of symmetrically arranged cartilaginous elements, the origin of which we have traced in Fishes, namely:—

One pair of basidorsalia.

One pair of basiventralia (with its lateral outgrowths = ribs or pleurapophyses,

and hæmal, ventral outgrowths = hæmal arches, chevrons, wedge-bones, hæmapophyses).

One pair of interdorsalia.

One pair of interventralia.

The first of these four pairs is always present and forms the neural arch. Of the other three pairs any one may be suppressed, sometimes even two in the same skleromere.

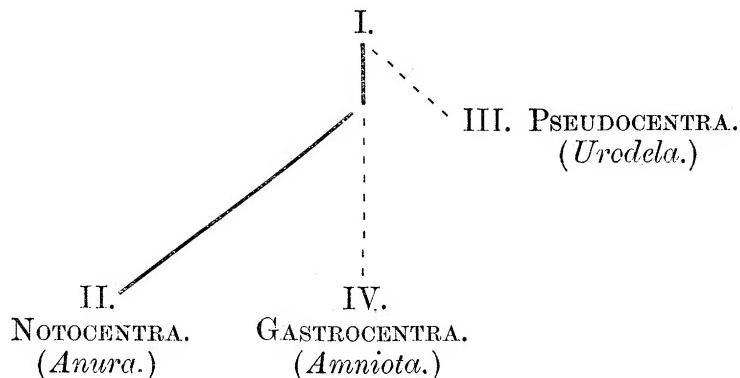
The vertebræ of the Amphibia and Amniota possess only arch-centra, because the chordal sheath takes no share in their formation.

According to the composition of these arco-genous centra or bodies, we distinguish the following lines of evolution :—

- I. All the four pairs of arcualia are present as separate pieces, of which the interventralia are the smallest, e.g., tail of *Archegosaurus*, *Sphenosaurus*, *Chelydosaurus*.
- II. The interventralia are suppressed.
 - A. The other three pieces remain separate, and the interdorsalia tend to form the centrum (NOTOCENTROUS type), e.g., trunk of *Euchirosaurus*, *Archegosaurus*, *Actinodon*, *Trimerorhachis*.
 - B. The three pairs of basidorsalia, interdorsalia and basiventralia co-ossify, e.g., trunk of *Anura*.
 - C. The interventralia and basiventralia are suppressed. Such "epichordal" vertebræ consist of dorsal elements only, e.g., trunk of *Pipa*, *Xenopus*, *Bombinator*.
- III. All the four pairs of arcualia are present, but the interbasalia form neutral zones of intervertebral cartilage (PSEUDOCENTROUS type), while—
 - A. The basidorsalia and basiventralia fuse together and form the middle of the vertebral body, e.g., tail of *Urodea*.
 - B. The basiventralia are suppressed, e.g., trunk of *Urodea*.
- IV. The interdorsalia are reduced. The interventralia are enlarged and form the centrum. (GASTROCENTROUS type.)
 - A. The three remaining components ossify separately and remain separate; the basiventralia are still large and carry most of the neural arch. (All the vertebræ of *Eryops*, *Cricotus*, the atlas of the Amniota.)
 - B. The centrum is much enlarged, forms the whole of the "body," and carries the neural arch (neurocentral suture). The basiventralia are much reduced and form the "intervertebral disks" or menisci, attached to the cranial end of the centrum; when less reduced, they appear as the so-called wedge-bones, "intercentra," or chevrons. (Trunk and tail of most Amniota.)

- c. The centrum and the neural arches alone constitute the vertebra. The basiventrals are lost completely. (Trunk of many Amniota, for instance, the thoracic and lumbar vertebræ of lizards, caudals of many mammalia and birds.)

The phylogeny of these modifications may be expressed as follows :—



The *ribs* are homologous structures throughout the Vertebrata. They are lateral distal outgrowths of the original basiventralia, with which they later on form joints, and they ossify independently.

The "chevrons," the bony arms or arches which enclose the caudal canal, are more ventral or median outgrowths of the same basiventralia and are to be called hæmapophyses. They are possibly serially homologous with the visceral arches, but any attempt to homologize them with, or to consider them as distal outgrowths of, the interventralia, results in failure. Ribs and hæmapophyses are not homologous structures, although both are ventral arches in a general sense.

The ribs are originally attached by their capitula, to the basiventralia ; the tubercular attachment to the neural arch is a secondary acquisition. When the basiventralia are reduced, the ribs either retain their old attachment and appear henceforth as "intervertebral" organs, *e.g.*, in many mammalia, in the anterior cervicals of *Hatteria*, and in many vertebræ of *Chelonia* ; or they transfer their attachment backwards upon the centrum, in some cases even upon the neural arches.

The *spinal nerves* arise originally in a transverse level behind the basidorsalia and in front of the interdorsalia, *i.e.*, intravertebrally. Each nerve issues behind, or through the neural arch of the vertebra to which it genetically belongs. The first spinal nerve, when it is a *N. sub-occipitalis* (although this nerve is not in all Vertebrata the same serial entity) has lost its vertebra, the latter being added to the skull, either completely, without leaving post-cranial remnants (*Amniota*), or incompletely, and in this case the ventral arcualia, probably the interventralia only, are added to the first vertebra as an odontoid-like process (*Urodeles*).

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